Preface

Biology is designed for multi-semester biology courses for science majors. It is grounded on an evolutionary basis and includes exciting features that highlight careers in the biological sciences and everyday applications of the concepts at hand. To meet the needs of today's instructors and students, some content has been strategically condensed while maintaining the overall scope and coverage of traditional texts for this course. Instructors can customize the book, adapting it to the approach that works best in their classroom. Biology also includes an innovative art program that incorporates critical thinking and clicker questions to help students understand—and apply—key concepts.

Welcome to *Biology*, an OpenStax resource. This textbook was written to increase student access to high-quality learning materials, maintaining highest standards of academic rigor at little to no cost.

About OpenStax

OpenStax is a nonprofit based at Rice University, and it's our mission to improve student access to education. Our first openly licensed college textbook was published in 2012, and our library has since scaled to over 20 books for college and AP courses used by hundreds of thousands of students. Our adaptive learning technology, designed to improve learning outcomes through personalized educational paths, is being piloted in college courses throughout the country. Through our partnerships with philanthropic foundations and our alliance with other educational resource organizations, OpenStax is breaking down the most common barriers to learning and empowering students and instructors to succeed.

About OpenStax's Resources

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Format

You can access this textbook for free in web view or PDF through openstax.org, and in low-cost print and iBooks editions.

About Biology

Biology is designed to cover the scope and sequence requirements of a typical two-semester biology course for science majors. The text provides comprehensive coverage of foundational research and core biology concepts through an evolutionary lens. *Biology* includes rich features that engage students in scientific inquiry, highlight careers in the biological sciences, and offer everyday applications. The book also includes clicker questions to help students understand—and apply—key concepts.

Coverage and Scope

In developing *Biology*, we listened to hundreds of General Biology instructors who readily provided feedback about their courses, students, challenges, and hopes for innovation. The expense of textbooks and related items did prove to be a barrier to learning. But more importantly, these teachers suggested improvements for the textbook, which would ultimately lead to more meaningful and memorable learning experiences for students.

The result is a book that addresses a core organizational reality of the course and its materials—the sheer breadth of the topical coverage. We provide a thorough treatment of biology's foundational concepts while condensing selected topics in response to the market's request for a textbook with a scope that is manageable for instructors and students alike. We also strive to make biology, as a discipline, interesting and accessible to students. In addition to a comprehensive coverage of core concepts and foundational research, we have incorporated features that draw learners into the discipline in meaningful ways.

The pedagogical choices, chapter arrangements, and learning objective fulfillment were developed and vetted with the feedback of another one hundred reviewers, who thoroughly read the material and offered detailed critical commentary.

Unit 1: **The Chemistry of Life**. Our opening unit introduces students to the sciences, including the scientific method and the fundamental concepts of chemistry and physics that provide a framework within which learners comprehend biological processes.

Unit 2: **The Cell**. Students will gain solid understanding of the structures, functions, and processes of the most basic unit of life: the cell.

Unit 3: **Genetics**. Our comprehensive genetics unit takes learners from the earliest experiments that revealed the basis of genetics through the intricacies of DNA to current applications in the emerging studies of biotechnology and genomics.

Unit 4: **Evolutionary Processes**. The core concepts of evolution are discussed in this unit with examples illustrating evolutionary processes. Additionally, the evolutionary basis of biology reappears throughout the textbook in general discussion and is reinforced through special call-out features highlighting specific evolution-based topics.

Unit 5: **Biological Diversity**. The diversity of life is explored with detailed study of various organisms and discussion of emerging phylogenetic relationships. This unit moves from viruses to living organisms like bacteria, discusses the organisms formerly grouped as protists, and devotes multiple chapters to plant and animal life.

Unit 6: **Plant Structure and Function**. Our plant unit thoroughly covers the fundamental knowledge of plant life essential to an introductory biology course.

Unit 7: **Animal Structure and Function**. An introduction to the form and function of the animal body is followed by chapters on specific body systems and processes. This unit touches on the biology of all organisms while maintaining an engaging focus on human anatomy and physiology that helps students connect to the topics.

Unit 8: **Ecology**. Ecological concepts are broadly covered in this unit, with features highlighting localized, real-world issues of conservation and biodiversity.

Pedagogical Foundation and Features

Biology is grounded in a solid scientific base, with features that engage the students in scientific inquiry, including:

Evolution Connection features uphold the importance of evolution to all biological study through discussions like "The Evolution of Metabolic Pathways" and "Algae and Evolutionary Paths to Photosynthesis."

Scientific Method Connection call-outs walk students through actual or thought experiments that elucidate the steps of the scientific process as applied to the topic. Features include "Determining the Time Spent in Cell Cycle Stages" and "Testing the Hypothesis of Independent Assortment."

Career Connection features present information on a variety of careers in the biological sciences, introducing students to the educational requirements and day-to-day work life of a variety of professions, such as microbiologist, ecologist, neurologist, and forensic scientist.

Everyday Connection features tie biological concepts to emerging issues and discuss science in terms of everyday life. Topics include "Chesapeake Bay" and "Can Snail Venom Be Used as a Pharmacological Pain Killer?"

Art and Animations That Engage

Our art program takes a straightforward approach designed to help students learn the concepts of biology through simple, effective illustrations, photos, and micrographs. *Biology* also incorporates links to relevant animations and interactive exercises that help bring biology to life for students.

Art Connection features call out core figures in each chapter for student study. Questions about key figures, including clicker questions that can be used in the classroom, engage students' critical thinking to ensure genuine understanding.

Link to Learning features direct students to online interactive exercises and animations to add a fuller context to core content.

Additional Resources

Student and Instructor Resources

We've compiled additional resources for both students and instructors, including Getting Started Guides, an instructor solution manual, supplemental test items, and PowerPoint slides. Instructor resources require a verified instructor account, which can be requested on your openstax.org log-in. Take advantage of these resources to supplement your OpenStax book.

Partner Resources

OpenStax Partners are our allies in the mission to make high-quality learning materials affordable and accessible to students and instructors everywhere. Their tools integrate seamlessly with our OpenStax titles at a low cost. To access the partner resources for your text, visit your book page on openstax.org.

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Introduction

class="introduction"

Certain prokaryotes can live in extreme environments such as the Morning Glory pool, a hot spring in Yellowstone National Park. The spring's vivid blue color is from the prokaryotes that thrive in its very hot waters. (credit: modification of work by Jon Sullivan)

In the recent past, scientists grouped living things into five kingdoms—animals, plants, fungi, protists, and prokaryotes—based on several criteria, such as the absence or presence of a nucleus and other membrane-bound organelles, the absence or presence of cell walls, multicellularity, and so on. In the late 20th century, the pioneering work of Carl Woese and others compared sequences of small-subunit ribosomal RNA (SSU rRNA), which resulted in a more fundamental way to group organisms on Earth. Based on differences in the structure of cell membranes and in rRNA, Woese and his colleagues proposed that all life on Earth evolved along three lineages, called domains. The domain Bacteria comprises all organisms in the kingdom Bacteria, the domain Archaea comprises the rest of the prokaryotes, and the domain Eukarya comprises all eukaryotes—including organisms in the kingdoms Animalia, Plantae, Fungi, and Protista.

Two of the three domains—Bacteria and Archaea—are prokaryotic. Prokaryotes were the first inhabitants on Earth, appearing 3.5 to 3.8 billion years ago. These organisms are abundant and ubiquitous; that is, they are present everywhere. In addition to inhabiting moderate environments, they are found in extreme conditions: from boiling springs to permanently frozen environments in Antarctica; from salty environments like the Dead Sea to environments under tremendous pressure, such as the depths of the ocean;

and from areas without oxygen, such as a waste management plant, to radioactively contaminated regions, such as Chernobyl. Prokaryotes reside in the human digestive system and on the skin, are responsible for certain illnesses, and serve an important role in the preparation of many foods.

Prokaryotic Diversity
By the end of this section, you will be able to:

- Describe the evolutionary history of prokaryotes
- Discuss the distinguishing features of extremophiles
- Explain why it is difficult to culture prokaryotes

Prokaryotes are ubiquitous. They cover every imaginable surface where there is sufficient moisture, and they live on and inside of other living things. In the typical human body, prokaryotic cells outnumber human body cells by about ten to one. They comprise the majority of living things in all ecosystems. Some prokaryotes thrive in environments that are inhospitable for most living things. Prokaryotes recycle **nutrients**—essential substances (such as carbon and nitrogen)—and they drive the evolution of new ecosystems, some of which are natural and others man-made. Prokaryotes have been on Earth since long before multicellular life appeared.

Prokaryotes, the First Inhabitants of Earth

When and where did life begin? What were the conditions on Earth when life began? Prokaryotes were the first forms of life on Earth, and they existed for billions of years before plants and animals appeared. The Earth and its moon are thought to be about 4.54 billion years old. This estimate is based on evidence from radiometric dating of meteorite material together with other substrate material from Earth and the moon. Early Earth had a very different atmosphere (contained less molecular oxygen) than it does today and was subjected to strong radiation; thus, the first organisms would have flourished where they were more protected, such as in ocean depths or beneath the surface of the Earth. At this time too, strong volcanic activity was common on Earth, so it is likely that these first organisms—the first prokaryotes—were adapted to very high temperatures. Early Earth was prone to geological upheaval and volcanic eruption, and was subject to bombardment by mutagenic radiation from the sun. The first organisms were prokaryotes that could withstand these harsh conditions.

Microbial Mats

Microbial mats or large biofilms may represent the earliest forms of life on Earth; there is fossil evidence of their presence starting about 3.5 billion years ago. A **microbial mat** is a multi-layered sheet of prokaryotes ([link]) that includes mostly bacteria, but also archaea. Microbial mats are a few centimeters thick, and they typically grow where different types of materials interface, mostly on moist surfaces. The various types of prokaryotes that comprise them carry out different metabolic pathways, and that is the reason for their various colors. Prokaryotes in a microbial mat are held together by a glue-like sticky substance that they secrete called extracellular matrix.

The first microbial mats likely obtained their energy from chemicals found near hydrothermal vents. A **hydrothermal vent** is a breakage or fissure in the Earth's surface that releases geothermally heated water. With the evolution of photosynthesis about 3 billion years ago, some prokaryotes in microbial mats came to use a more widely available energy source—sunlight—whereas others were still dependent on chemicals from hydrothermal vents for energy and food.

(a)   (b)
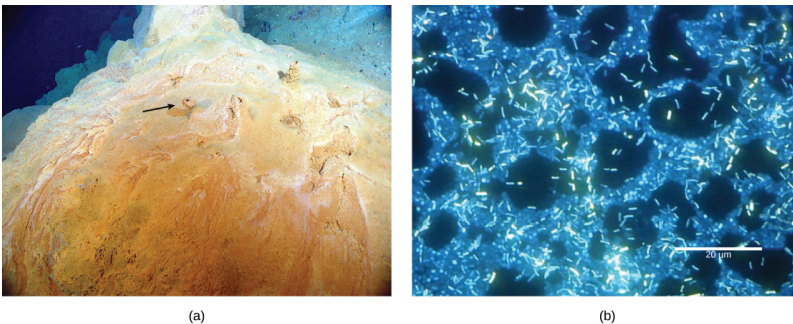
This (a) microbial mat, about one meter in diameter, grows over a hydrothermal vent in the Pacific Ocean in a region known as the "Pacific Ring of Fire." The mat helps retain microbial nutrients. Chimneys such as the one indicated by the arrow allow gases to escape. (b) In this micrograph, bacteria are

visualized using fluorescence microscopy. (credit a: modification of work by Dr. Bob Embley, NOAA PMEL, Chief Scientist; credit b: modification of work by Ricardo Murga, Rodney Donlan, CDC; scale-bar data from Matt Russell)

Stromatolites

Fossilized microbial mats represent the earliest record of life on Earth. A **stromatolite** is a sedimentary structure formed when minerals are precipitated out of water by prokaryotes in a microbial mat ([link]). Stromatolites form layered rocks made of carbonate or silicate. Although most stromatolites are artifacts from the past, there are places on Earth where stromatolites are still forming. For example, growing stromatolites have been found in the Anza-Borrego Desert State Park in San Diego County, California.

(a)   (b)

(a) These living stromatolites are located in Shark Bay, Australia. (b) These fossilized stromatolites, found in Glacier National Park, Montana, are nearly 1.5 billion years old. (credit a: Robert Young; credit b: P. Carrara, NPS)

The Ancient Atmosphere

Evidence indicates that during the first two billion years of Earth's existence, the atmosphere was **anoxic**, meaning that there was no molecular oxygen. Therefore, only those organisms that can grow without oxygen—**anaerobic** organisms—were able to live. Autotrophic organisms that convert solar energy into chemical energy are called **phototrophs**, and they appeared within one billion years of the formation of Earth. Then, **cyanobacteria**, also known as blue-green algae, evolved from these simple phototrophs one billion years later. Cyanobacteria ([link]) began the oxygenation of the atmosphere. Increased atmospheric oxygen allowed the development of more efficient O_2-utilizing catabolic pathways. It also opened up the land to increased colonization, because some O_2 is converted into O_3 (ozone) and ozone effectively absorbs the ultraviolet light that would otherwise cause lethal mutations in DNA. Ultimately, the increase in O_2 concentrations allowed the evolution of other life forms.

This hot spring in Yellowstone National Park flows toward the foreground. Cyanobacteria in the spring are green, and as

water flows down the gradient, the intensity of the color increases as cell density increases. The water is cooler at the edges of the stream than in the center, causing the edges to appear greener. (credit: Graciela Brelles-Mariño)

Microbes Are Adaptable: Life in Moderate and Extreme Environments

Some organisms have developed strategies that allow them to survive harsh conditions. Prokaryotes thrive in a vast array of environments: Some grow in conditions that would seem very normal to us, whereas others are able to thrive and grow under conditions that would kill a plant or animal. Almost all prokaryotes have a cell wall, a protective structure that allows them to survive in both hyper- and hypo-osmotic conditions. Some soil bacteria are able to form endospores that resist heat and drought, thereby allowing the organism to survive until favorable conditions recur. These adaptations, along with others, allow bacteria to be the most abundant life form in all terrestrial and aquatic ecosystems.

Other bacteria and archaea are adapted to grow under extreme conditions and are called **extremophiles**, meaning "lovers of extremes." Extremophiles have been found in all kinds of environments: the depth of the oceans, hot springs, the Artic and the Antarctic, in very dry places, deep inside Earth, in harsh chemical environments, and in high radiation environments ([link]), just to mention a few. These organisms give us a better understanding of prokaryotic diversity and open up the possibility of finding new prokaryotic species that may lead to the discovery of new therapeutic drugs or have industrial applications. Because they have specialized adaptations that allow them to live in extreme conditions, many extremophiles cannot survive in moderate environments. There are many different groups of extremophiles: They are identified based on the

conditions in which they grow best, and several habitats are extreme in multiple ways. For example, a soda lake is both salty and alkaline, so organisms that live in a soda lake must be both alkaliphiles and halophiles ([link]). Other extremophiles, like **radioresistant** organisms, do not prefer an extreme environment (in this case, one with high levels of radiation), but have adapted to survive in it ([link]).

Extremophiles and Their Preferred Conditions	
Extremophile Type	**Conditions for Optimal Growth**
Acidophiles	pH 3 or below
Alkaliphiles	pH 9 or above
Thermophiles	Temperature 60–80 °C (140–176 °F)
Hyperthermophiles	Temperature 80–122 °C (176–250 °F)
Psychrophiles	Temperature of -15-10 °C (5-50 °F) or lower
Halophiles	Salt concentration of at least 0.2 M
Osmophiles	High sugar concentration
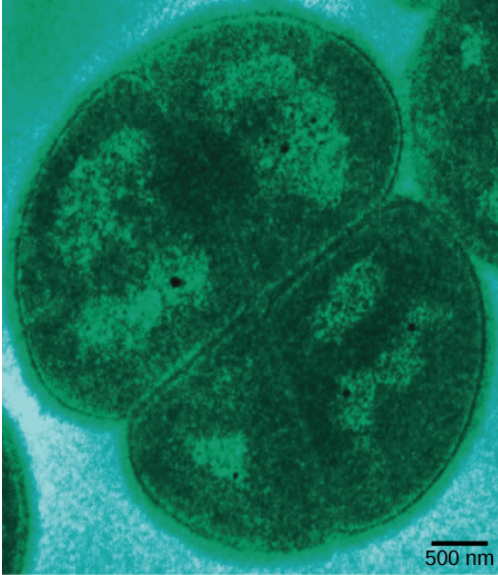
Deinococcus radiodurans, visualized in this false color transmission electron micrograph, is a prokaryote that can tolerate very high doses of ionizing radiation. It has developed DNA repair mechanisms that allow it to reconstruct its chromosome even if it has been broken into hundreds of pieces by radiation or heat. (credit: modification of work by Michael Daly; scale-bar data from Matt Russell)

Prokaryotes in the Dead Sea

One example of a very harsh environment is the Dead Sea, a hypersaline basin that is located between Jordan and Israel. Hypersaline environments are essentially concentrated seawater. In the Dead Sea, the sodium concentration is 10 times higher than that of seawater, and the water contains high levels of magnesium (about 40 times higher than in seawater) that would be toxic to most living things. Iron, calcium, and magnesium, elements that form divalent ions (Fe^{2+}, Ca^{2+}, and Mg^{2+}), produce what is commonly referred to as "hard" water. Taken together, the high concentration of divalent cations, the acidic pH (6.0), and the intense solar radiation flux make the Dead Sea a unique, and uniquely hostile, ecosystem[footnote] ([link]).

Bodaker, I, Itai, S, Suzuki, MT, Feingersch, R, Rosenberg, M, Maguire, ME, Shimshon, B, and others. Comparative community genomics in the Dead Sea: An increasingly extreme environment. *The ISME Journal* 4 (2010): 399–407, doi:10.1038/ismej.2009.141. published online 24 December 2009.

What sort of prokaryotes do we find in the Dead Sea? The extremely salt-tolerant bacterial mats include *Halobacterium, Haloferax volcanii* (which is found in other locations, not only the Dead Sea), *Halorubrum sodomense*, and *Halobaculum gomorrense*, and the archaea *Haloarcula marismortui*, among others.
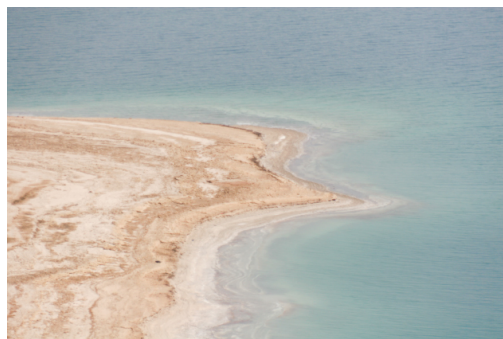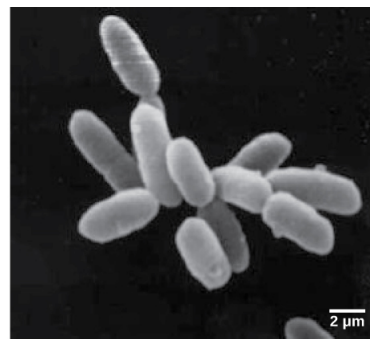
(a)   (b)

(a) The Dead Sea is hypersaline. Nevertheless, salt-tolerant bacteria thrive in this sea. (b) These halobacteria cells can form salt-tolerant bacterial

mats. (credit a: Julien Menichini; credit b: NASA; scale-bar data from Matt Russell)

Unculturable Prokaryotes and the Viable-but-Non-Culturable State

Microbiologists typically grow prokaryotes in the laboratory using an appropriate culture medium containing all the nutrients needed by the target organism. The medium can be liquid, broth, or solid. After an incubation time at the right temperature, there should be evidence of microbial growth ([link]). The process of culturing bacteria is complex and is one of the greatest discoveries of modern science. German physician Robert Koch is credited with discovering the techniques for pure culture, including staining and using growth media. His assistant Julius Petri invented the Petri dish whose use persists in today's laboratories. Koch worked primarily with the *Mycobacterium tuberculosis* bacterium that causes tuberculosis and developed postulates to identify disease-causing organisms that continue to be widely used in the medical community. Koch's postulates include that an organism can be identified as the cause of disease when it is present in all infected samples and absent in all healthy samples, and it is able to reproduce the infection after being cultured multiple times. Today, cultures remain a primary diagnostic tool in medicine and other areas of molecular biology.

In these agar plates, the

growth medium is supplemented with red blood cells. Blood agar becomes transparent in the presence of hemolytic *Streptococcus*, which destroys red blood cells and is used to diagnose *Streptococcus* infections. The plate on the left is inoculated with non-hemolytic *Staphylococcus* (large white colonies), and the plate on the right is inoculated with hemolytic *Streptococcus* (tiny clear colonies). If you look closely at the right plate, you can see that the agar surrounding the bacteria has turned clear. (credit: Bill Branson, NCI)

Some prokaryotes, however, cannot grow in a laboratory setting. In fact, over 99 percent of bacteria and archaea are unculturable. For the most part, this is due to a lack of knowledge as to what to feed these organisms and how to grow them; they have special requirements for growth that remain unknown to scientists, such as needing specific micronutrients, pH, temperature, pressure, co-factors, or co-metabolites. Some bacteria cannot be cultured because they are obligate intracellular parasites and cannot be grown outside a host cell.

In other cases, culturable organisms become unculturable under stressful conditions, even though the same organism could be cultured previously. Those organisms that cannot be cultured but are not dead are in a **viable-but-non-culturable** (VBNC) state. The VBNC state occurs when prokaryotes respond to environmental stressors by entering a dormant state

that allows their survival. The criteria for entering into the VBNC state are not completely understood. In a process called **resuscitation**, the prokaryote can go back to "normal" life when environmental conditions improve.

Is the VBNC state an unusual way of living for prokaryotes? In fact, most of the prokaryotes living in the soil or in oceanic waters are non-culturable. It has been said that only a small fraction, perhaps one percent, of prokaryotes can be cultured under laboratory conditions. If these organisms are non-culturable, then how is it known whether they are present and alive? Microbiologists use molecular techniques, such as the polymerase chain reaction (PCR), to amplify selected portions of DNA of prokaryotes, demonstrating their existence. Recall that PCR can make billions of copies of a DNA segment in a process called amplification.

The Ecology of Biofilms

Until a couple of decades ago, microbiologists used to think of prokaryotes as isolated entities living apart. This model, however, does not reflect the true ecology of prokaryotes, most of which prefer to live in communities where they can interact. A **biofilm** is a microbial community ([link]) held together in a gummy-textured matrix that consists primarily of polysaccharides secreted by the organisms, together with some proteins and nucleic acids. Biofilms grow attached to surfaces. Some of the best-studied biofilms are composed of prokaryotes, although fungal biofilms have also been described as well as some composed of a mixture of fungi and bacteria.

Biofilms are present almost everywhere: they can cause the clogging of pipes and readily colonize surfaces in industrial settings. In recent, large-scale outbreaks of bacterial contamination of food, biofilms have played a major role. They also colonize household surfaces, such as kitchen counters, cutting boards, sinks, and toilets, as well as places on the human body, such as the surfaces of our teeth.

Interactions among the organisms that populate a biofilm, together with their protective exopolysaccharidic (EPS) environment, make these

communities more robust than free-living, or planktonic, prokaryotes. The sticky substance that holds bacteria together also excludes most antibiotics and disinfectants, making biofilm bacteria hardier than their planktonic counterparts. Overall, biofilms are very difficult to destroy because they are resistant to many common forms of sterilization.
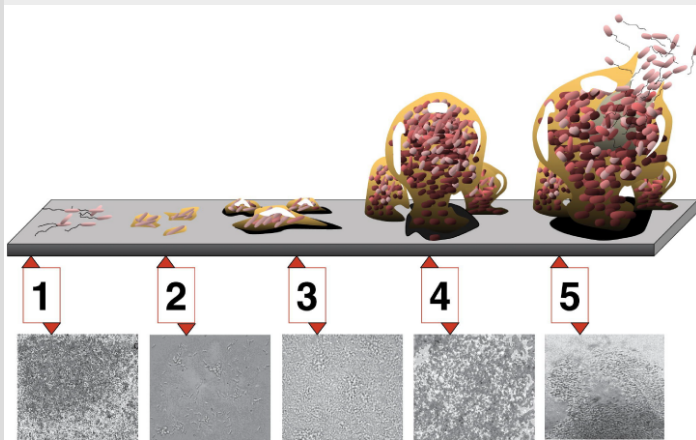
Five stages of biofilm development are shown. During stage 1, initial attachment, bacteria adhere to a solid surface via weak van der Waals interactions. During stage 2, irreversible attachment, hairlike appendages called pili permanently anchor the bacteria to the surface. During stage 3, maturation I, the biofilm grows through cell division and recruitment of other bacteria. An extracellular matrix composed primarily of polysaccharides holds the biofilm together. During stage 4, maturation II, the biofilm continues to grow and takes on a more complex shape. During stage 5, dispersal, the

biofilm matrix is partly broken down, allowing some bacteria to escape and colonize another surface. Micrographs of a *Pseudomonas aeruginosa* biofilm in each of the stages of development are shown. (credit: D. Davis, Don Monroe, PLoS)

Compared to free-floating bacteria, bacteria in biofilms often show increased resistance to antibiotics and detergents. Why do you think this might be the case?

Section Summary

Prokaryotes existed for billions of years before plants and animals appeared. Hot springs and hydrothermal vents may have been the environments in which life began. Microbial mats are thought to represent the earliest forms of life on Earth, and there is fossil evidence of their presence about 3.5 billion years ago. A microbial mat is a multi-layered sheet of prokaryotes that grows at interfaces between different types of material, mostly on moist surfaces. During the first 2 billion years, the atmosphere was anoxic and only anaerobic organisms were able to live. Cyanobacteria evolved from early phototrophs and began the oxygenation of the atmosphere. The increase in oxygen concentration allowed the evolution of other life forms. Fossilized microbial mats are called stromatolites and consist of laminated organo-sedimentary structures formed by precipitation of minerals by prokaryotes. They represent the earliest fossil record of life on Earth.

Bacteria and archaea grow in virtually every environment. Those that survive under extreme conditions are called extremophiles (extreme lovers). Some prokaryotes cannot grow in a laboratory setting, but they are not dead. They are in the viable-but-non-culturable (VBNC) state. The VBNC state occurs when prokaryotes enter a dormant state in response to

environmental stressors. Most prokaryotes are social and prefer to live in communities where interactions take place. A biofilm is a microbial community held together in a gummy-textured matrix.

Art Connections

Exercise:

Problem:

[link] Compared to free-floating bacteria, bacteria in biofilms often show increased resistance to antibiotics and detergents. Why do you think this might be the case?

Solution:

[link] The extracellular matrix and outer layer of cells protects the inner bacteria. The close proximity of cells also facilitates lateral gene transfer, a process by which genes such as antibiotic resistance genes are transferred from one bacterium to another. And even if lateral gene transfer does not occur, one bacterium that produces an exo-enzyme that destroys antibiotic may save neighboring bacteria.

Review Questions

Exercise:

Problem:

The first forms of life on Earth were thought to be_____.

- a. single-celled plants
- b. prokaryotes
- c. insects
- d. large animals such as dinosaurs

Solution:

A

Exercise:

Problem: Microbial mats _____.

    a. are the earliest forms of life on Earth
    b. obtained their energy and food from hydrothermal vents
    c. are multi-layered sheet of prokaryotes including mostly bacteria
       but also archaea
    d. all of the above

Solution:

D

Exercise:

Problem: The first organisms that oxygenated the atmosphere were

    a. cyanobacteria
    b. phototrophic organisms
    c. anaerobic organisms
    d. all of the above

Solution:

A

Exercise:

Problem: Halophiles are organisms that require_____.

    a. a salt concentration of at least 0.2 M
    b. high sugar concentration
    c. the addition of halogens
    d. all of the above

Solution:

A

Free Response

Exercise:

Problem:

Describe briefly how you would detect the presence of a non-culturable prokaryote in an environmental sample.

Solution:

As the organisms are non-culturable, the presence could be detected through molecular techniques, such as PCR.

Exercise:

Problem:

Why do scientists believe that the first organisms on Earth were extremophiles?

Solution:

Because the environmental conditions on Earth were extreme: high temperatures, lack of oxygen, high radiation, and the like.

Glossary

acidophile
    organism with optimal growth pH of three or below

alkaliphile

organism with optimal growth pH of nine or above

anaerobic
refers to organisms that grow without oxygen

anoxic
without oxygen

biofilm
a microbial community growing together on a surface, often held together with a gummy matrix

cyanobacteria
bacteria that evolved from early phototrophs and oxygenated the atmosphere; also known as blue-green algae

extremophile
organism that grows under extreme or harsh conditions

halophile
organism that require a salt concentration of at least 0.2 M

hydrothermal vent
fissure in Earth's surface that releases geothermally heated water

hyperthermophile
organism that grows at temperatures between 80–122 °C

microbial mat
multi-layered sheet of prokaryotes that may include bacteria and archaea

nutrient
essential substances for growth, such as carbon and nitrogen

osmophile
organism that grows in a high sugar concentration

phototroph

organism that is able to make its own food by converting solar energy to chemical energy

psychrophile
organism that grows at temperatures of -15 °C or lower

radioresistant
organism that grows in high levels of radiation

resuscitation
process by which prokaryotes that are in the VBNC state return to viability

stromatolite
layered sedimentary structure formed by precipitation of minerals by prokaryotes in microbial mats

thermophile
organism that lives at temperatures between 60–80 °C

viable-but-non-culturable (VBNC) state
survival mechanism of bacteria facing environmental stress conditions

Structure of Prokaryotes
By the end of this section, you will be able to:

- Describe the basic structure of a typical prokaryote
- Describe important differences in structure between Archaea and Bacteria

There are many differences between prokaryotic and eukaryotic cells. However, all cells have four common structures: the plasma membrane, which functions as a barrier for the cell and separates the cell from its environment; the cytoplasm, a jelly-like substance inside the cell; nucleic acids, the genetic material of the cell; and ribosomes, where protein synthesis takes place. Prokaryotes come in various shapes, but many fall into three categories: cocci (spherical), bacilli (rod-shaped), and spirilli (spiral-shaped) ([link]).
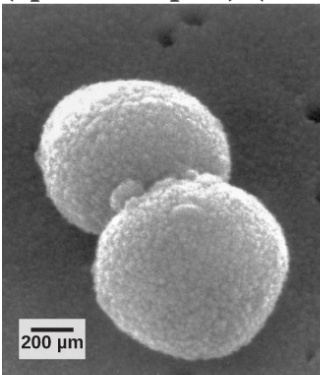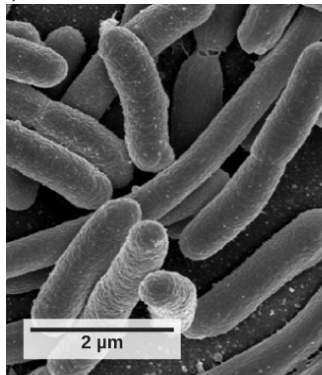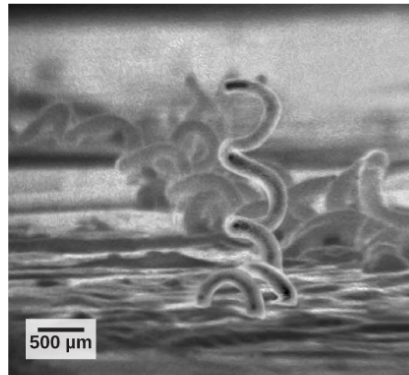
(a) (b) (c)

Prokaryotes fall into three basic categories based on their shape, visualized here using scanning electron microscopy: (a) cocci, or spherical (a pair is shown); (b) bacilli, or rod-shaped; and (c) spirilli, or spiral-shaped. (credit a: modification of work by Janice Haney Carr, Dr. Richard Facklam, CDC; credit c: modification of work by Dr. David Cox; scale-bar data from Matt Russell)

The Prokaryotic Cell

Recall that prokaryotes ([link]) are unicellular organisms that lack organelles or other internal membrane-bound structures. Therefore, they do not have a nucleus but instead generally have a single chromosome—a piece of circular, double-stranded DNA located in an area of the cell called the nucleoid. Most prokaryotes have a cell wall outside the plasma membrane.
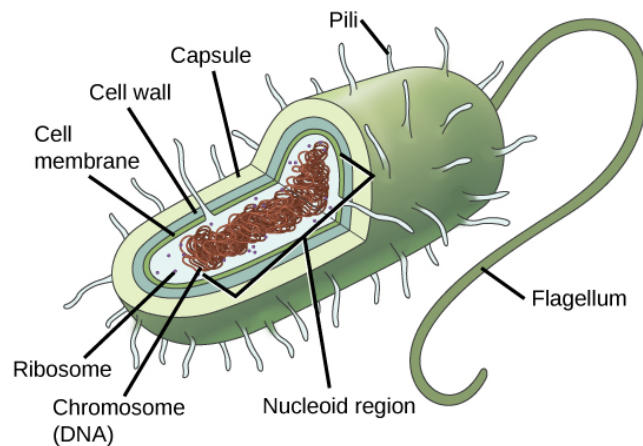
The features of a typical prokaryotic cell are shown.

Recall that prokaryotes are divided into two different domains, Bacteria and Archaea, which together with Eukarya, comprise the three domains of life ([link]).
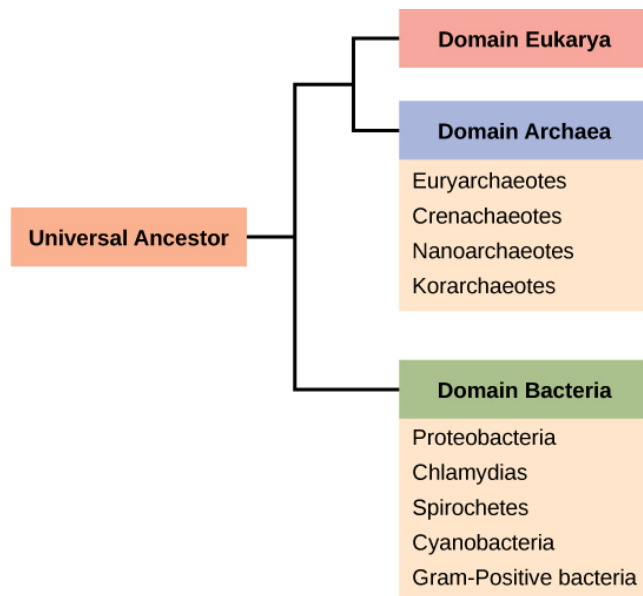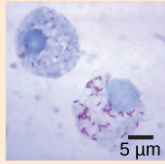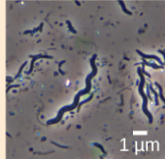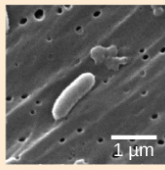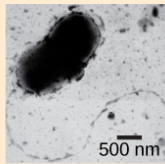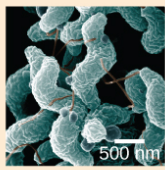
Bacteria and Archaea are both prokaryotes but differ enough to be placed in separate domains. An ancestor of modern Archaea is believed to have given rise to Eukarya, the third domain of life. Archaeal and bacterial phyla are shown; the evolutionary relationship between these phyla is still open to debate.

The composition of the cell wall differs significantly between the domains Bacteria and Archaea. The composition of their cell walls also differs from the eukaryotic cell walls found in plants (cellulose) or fungi and insects (chitin). The cell wall functions as a protective layer, and it is responsible for the organism's shape. Some bacteria have an outer **capsule** outside the cell wall. Other structures are present in some prokaryotic species, but not in others ([link]). For example, the capsule found in some species enables the organism to attach to surfaces, protects it from dehydration and attack by phagocytic cells, and makes pathogens more resistant to our immune responses. Some species also have flagella (singular, flagellum) used for
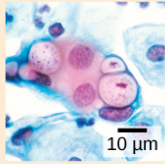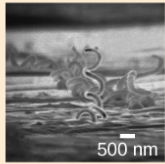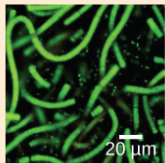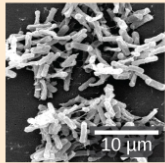
locomotion, and **pili** (singular, pilus) used for attachment to surfaces. Plasmids, which consist of extra-chromosomal DNA, are also present in many species of bacteria and archaea.

Characteristics of phyla of Bacteria are described in [link] and [link]; Archaea are described in [link].

Bacteria of Phylum Proteobacteria		
Class	**Representative organisms**	**Representative micrograph**
Alpha Proteobacteria Some species are photoautotrophic but some are symbionts of plants and animals and others are pathogens. Eukaryotic mitochondria are thought be derived from bacteria in this group.	*Rhizobium* Nitrogen-fixing endosymbiont associated with the roots of legumes *Rickettsia* Obligate intracellular parasite that causes typhus and Rocky Mountain Spotted Fever (but not rickets, which is caused by Vitamin C deficiency)	 *Rickettsia rickettsia,* stained red, grow inside a host cell.
Beta Proteobacteria This group of bacteria is diverse. Some species play an important role in the nitrogen cycle.	*Nitrosomas* Species from this group oxidize ammonia into nitrite. *Spirillum minus* Causes rat-bite fever	 *Spirillum minus*
Gamma Proteobacteria Many are beneficial symbionts that populate the human gut, but others are familiar human pathogens. Some species from this subgroup oxidize sulfur compounds.	*Escherichia coli* Normally beneficial microbe of the human gut, but some strains cause disease *Salmonella* Certain strains cause food poisoning or typhoid fever *Yersinia pestis* Causative agent of Bubonic plague *Psuedomonas aeruginosa* Causes lung infections *Vibrio cholera* Causative agent of cholera *Chromatium* Sulfur-producing bacteria that oxidize sulfur, producing H_2S	 *Vibrio cholera*
Delta Proteobacteria Some species generate a spore-forming fruiting body in adverse conditions. Others reduce sulfate and sulfur.	*Myxobacteria* Generate spore-forming fruiting bodies in adverse conditions *Desulfovibrio vulgaris* Aneorobic, sulfate-reducing bacterium	 *Desulfovibrio vulgaris*
Epsilon Proteobacteria Many species inhabit the digestive tract of animals as symbionts or pathogens. Bacteria from this group have been found in deep-sea hydrothermal vents and cold seep habitats.	*Campylobacter* Causes blood poisoning and intestinal inflammation *Heliobacter pylori* Causes stomach ulcers	 *Campylobacter*
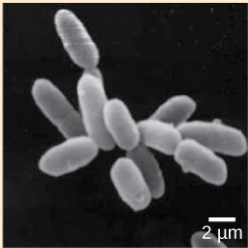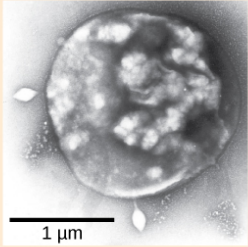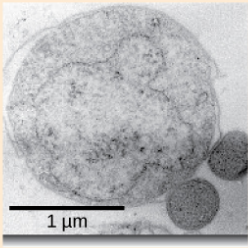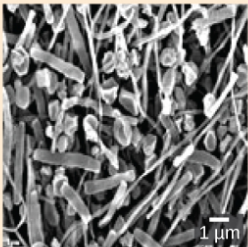
Phylum Proteobacteria is one of up to 52 bacteria phyla. Proteobacteria is further subdivided into five classes, Alpha through Epsilon. (credit "Rickettsia rickettsia": modification of work by CDC; credit "Spirillum minus": modification of work by Wolframm Adlassnig; credit "Vibrio cholera": modification of work by Janice Haney Carr, CDC; credit "Desulfovibrio

vulgaris": modification of work by Graham Bradley; credit "Campylobacter": modification of work by De Wood, Pooley, USDA, ARS, EMU; scale-bar data from Matt Russell)

Bacteria: Chlamydia, Spirochaetae, Cyanobacteria, and Gram-positive		
Phylum	Representative organisms	Representative micrograph
Chlamydias All members of this group are obligate intracellular parasites of animal cells. Cells walls lack peptidoglycan.	*Chlamydia trachomatis* Common sexually transmitted disease that can lead to blindness	 10 µm In this pap smear, *Chlamydia trachomatis* appear as pink inclusions inside cells.
Spirochetes Most members of this species, which has spiral-shaped cells, are free-living aneaerobes, but some are pathogenic. Flagella run lengthwise in the periplasmic space between the inner and outer membrane.	*Treponema pallidum* Causative agent of syphilis *Borrelia burgdorferi* Causative agent of Lyme disease	 500 nm *Treponema pallidum*
Cyanobacteria Also known as blue-green algae, these bacteria obtain their energy through photosynthesis. They are ubiquitous, found in terrestrial, marine, and freshwater environments. Eukaryotic chloroplasts are thought be derived from bacteria in this group.	*Prochlorococcus* Believed to be the most abundant photosynthetic organism on earth; responsible for generating half the world's oxygen	 20 µm *Phormidium*
Gram-positive Bacteria Soil-dwelling members of this subgroup decompose organic matter. Some species cause disease. They have a thick cell wall and lack an outer membrane.	*Bacillus anthracis* Causes anthrax *Clostridium botulinum* Causes Botulism *Clostridium difficile* Causes diarrhea during antibiotic therapy *Streptomyces* Many antibiotics, including streptomyocin, are derived from these bacteria. *Mycoplasmas* These tiny bacteria, the smallest known, lack a cell wall. Some are free-living, and some are pathogenic.	 10 µm *Clostridium difficile*

Chlamydia, Spirochetes, Cyanobacteria, and Gram-positive bacteria are described in this table. Note that bacterial shape is not phylum-dependent; bacteria within a phylum may be cocci,

rod-shaped, or spiral. (credit "Chlamydia trachomatis": modification of work by Dr. Lance Liotta Laboratory, NCI; credit "Treponema pallidum": modification of work by Dr. David Cox, CDC; credit "Phormidium": modification of work by USGS; credit "Clostridium difficile": modification of work by Lois S. Wiggs, CDC; scale-bar data from Matt Russell)

Archaea		
Phylum	**Representative organisms**	**Representative micrograph**
Euryarchaeota This phylum includes methanogens, which produce methane as a metabolic waste product, and halobacteria, which live in an extreme saline environment.	*Methanogens* Methane production causes flatulence in humans and other animals. *Halobacteria* Large blooms of this salt-loving archaea appear reddish due to the presence of bacterirhodopsin in the membrane. Bacteriorhodopsin is related to the retinal pigment rhodopsin.	 *Halobacterium* strain NRC-1
Crenarchaeota Members of the ubiquitous phylum play an important role in the fixation of carbon. Many members of this group are sulfur-dependent extremophiles. Some are thermophilic or hyperthermophilic.	*Sulfolobus* Members of this genus grow in volcanic springs at temperatures between 75° and 80°C and at a pH between 2 and 3.	 *Sulfolobus* being infected by bacteriophage
Nanoarchaeota This group currently contains only one species, *Nanoarchaeum equitans*.	*Nanoarchaeum equitans* This species was isolated from the bottom of the Atlantic Ocean and from a hydrothermal vent at Yellowstone National Park. It is an obligate symbiont with *Ignicoccus*, another species of archaea.	 *Nanoarchaeum equitans* (small dark spheres) are in contact with their larger host, *Ignicoccus*.
Korarchaeota Members of this phylum, considered to be one of the most primitive forms of life, have only been found in the Obsidian Pool, a hot spring at Yellowstone National Park.	No members of this species have been cultivated.	 This image shows a variety of korarchaeota species from the Obsidian Pool at Yellowstone National Park.

Archaea are separated into four phyla: the Korarchaeota, Euryarchaeota, Crenarchaeota, and Nanoarchaeota. (credit "Halobacterium": modification of work by NASA; credit "Nanoarchaeotum equitans": modification of work by Karl O. Stetter; credit "korarchaeota": modification of work by Office of Science of the U.S. Dept. of Energy; scale-bar data from Matt Russell)

The Plasma Membrane

The plasma membrane is a thin lipid bilayer (6 to 8 nanometers) that completely surrounds the cell and separates the inside from the outside. Its selectively permeable nature keeps ions, proteins, and other molecules within the cell and prevents them from diffusing into the extracellular environment, while other molecules may move through the membrane. Recall that the general structure of a cell membrane is a phospholipid bilayer composed of two layers of lipid molecules. In archaeal cell membranes, isoprene (phytanyl) chains linked to glycerol replace the fatty acids linked to glycerol in bacterial membranes. Some archaeal membranes are lipid monolayers instead of bilayers ([link]).
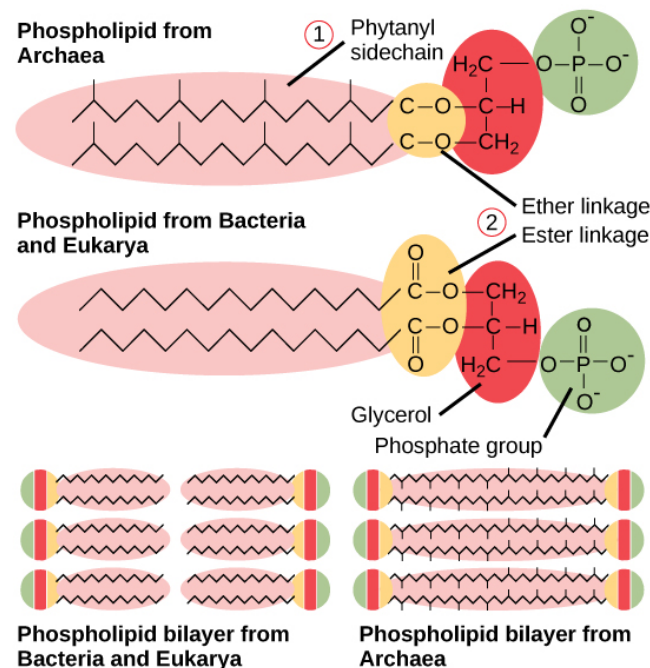
Archaeal phospholipids differ
from those found in Bacteria and

Eukarya in two ways. First, they have branched phytanyl sidechains instead of linear ones. Second, an ether bond instead of an ester bond connects the lipid to the glycerol.

The Cell Wall

The cytoplasm of prokaryotic cells has a high concentration of dissolved solutes. Therefore, the osmotic pressure within the cell is relatively high. The cell wall is a protective layer that surrounds some cells and gives them shape and rigidity. It is located outside the cell membrane and prevents osmotic lysis (bursting due to increasing volume). The chemical composition of the cell walls varies between archaea and bacteria, and also varies between bacterial species.

Bacterial cell walls contain **peptidoglycan**, composed of polysaccharide chains that are cross-linked by unusual peptides containing both L- and D-amino acids including D-glutamic acid and D-alanine. Proteins normally have only L-amino acids; as a consequence, many of our antibiotics work by mimicking D-amino acids and therefore have specific effects on bacterial cell wall development. There are more than 100 different forms of peptidoglycan. **S-layer** (surface layer) proteins are also present on the outside of cell walls of both archaea and bacteria.

Bacteria are divided into two major groups: **Gram positive** and **Gram negative**, based on their reaction to Gram staining. Note that all Gram-positive bacteria belong to one phylum; bacteria in the other phyla (Proteobacteria, Chlamydias, Spirochetes, Cyanobacteria, and others) are Gram-negative. The Gram staining method is named after its inventor, Danish scientist Hans Christian Gram (1853–1938). The different bacterial responses to the staining procedure are ultimately due to cell wall structure. Gram-positive organisms typically lack the outer membrane found in Gram-negative organisms ([link]). Up to 90 percent of the cell wall in Gram-

positive bacteria is composed of peptidoglycan, and most of the rest is composed of acidic substances called **teichoic acids**. Teichoic acids may be covalently linked to lipids in the plasma membrane to form lipoteichoic acids. Lipoteichoic acids anchor the cell wall to the cell membrane. Gram-negative bacteria have a relatively thin cell wall composed of a few layers of peptidoglycan (only 10 percent of the total cell wall), surrounded by an outer envelope containing lipopolysaccharides (LPS) and lipoproteins. This outer envelope is sometimes referred to as a second lipid bilayer. The chemistry of this outer envelope is very different, however, from that of the typical lipid bilayer that forms plasma membranes.

Note:
Art Connection
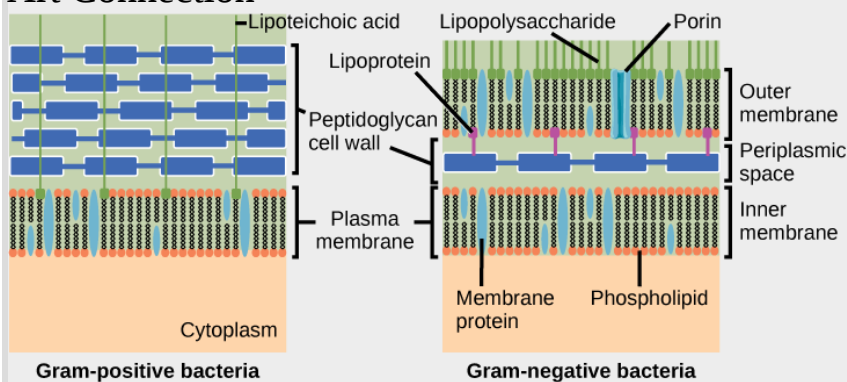
Bacteria are divided into two major groups: Gram positive and Gram negative. Both groups have a cell wall composed of peptidoglycan: in Gram-positive bacteria, the wall is thick, whereas in Gram-negative bacteria, the wall is thin. In Gram-negative bacteria, the cell wall is surrounded by an outer membrane that contains lipopolysaccharides and lipoproteins. Porins are proteins in this cell membrane that allow substances to pass through the outer membrane of Gram-negative bacteria. In Gram-positive bacteria, lipoteichoic acid anchors the cell wall to the cell membrane.

Which of the following statements is true?

a. Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.
b. Porins allow entry of substances into both Gram-positive and Gram-negative bacteria.
c. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
d. Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.

Archaean cell walls do not have peptidoglycan. There are four different types of Archaean cell walls. One type is composed of **pseudopeptidoglycan**, which is similar to peptidoglycan in morphology but contains different sugars in the polysaccharide chain. The other three types of cell walls are composed of polysaccharides, glycoproteins, or pure protein.

Structural Differences and Similarities between Bacteria and Archaea		
Structural Characteristic	Bacteria	Archaea

Structural Differences and Similarities between Bacteria and Archaea		
Structural Characteristic	**Bacteria**	**Archaea**
Cell type	Prokaryotic	Prokaryotic
Cell morphology	Variable	Variable
Cell wall	Contains peptidoglycan	Does not contain peptidoglycan
Cell membrane type	Lipid bilayer	Lipid bilayer or lipid monolayer
Plasma membrane lipids	Fatty acids	Phytanyl groups

Reproduction

Reproduction in prokaryotes is asexual and usually takes place by binary fission. Recall that the DNA of a prokaryote exists as a single, circular chromosome. Prokaryotes do not undergo mitosis. Rather the chromosome is replicated and the two resulting copies separate from one another, due to the growth of the cell. The prokaryote, now enlarged, is pinched inward at its equator and the two resulting cells, which are clones, separate. Binary fission does not provide an opportunity for genetic recombination or genetic diversity, but prokaryotes can share genes by three other mechanisms.

In **transformation**, the prokaryote takes in DNA found in its environment that is shed by other prokaryotes. If a nonpathogenic bacterium takes up DNA for a toxin gene from a pathogen and incorporates the new DNA into its own chromosome, it too may become pathogenic. In **transduction**, bacteriophages, the viruses that infect bacteria, sometimes also move short pieces of chromosomal DNA from one bacterium to another. Transduction

results in a recombinant organism. Archaea are not affected by bacteriophages but instead have their own viruses that translocate genetic material from one individual to another. In **conjugation**, DNA is transferred from one prokaryote to another by means of a pilus, which brings the organisms into contact with one another. The DNA transferred can be in the form of a plasmid or as a hybrid, containing both plasmid and chromosomal DNA. These three processes of DNA exchange are shown in [link].

Reproduction can be very rapid: a few minutes for some species. This short generation time coupled with mechanisms of genetic recombination and high rates of mutation result in the rapid evolution of prokaryotes, allowing them to respond to environmental changes (such as the introduction of an antibiotic) very quickly.

(a) Transformation   (b) Transduction   (c) Conjugation
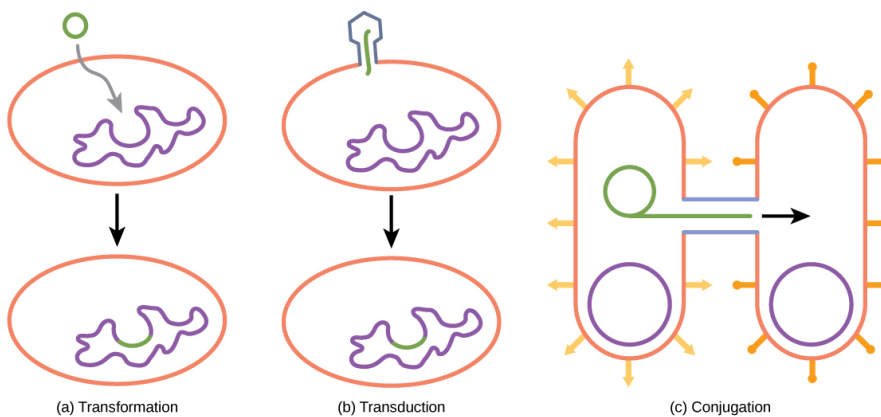
Besides binary fission, there are three other mechanisms by which prokaryotes can exchange DNA. In (a) transformation, the cell takes up prokaryotic DNA directly from the environment. The DNA may remain separate as plasmid DNA or be incorporated into the host genome. In (b) transduction, a bacteriophage injects DNA into the cell that contains a small fragment of DNA from a different prokaryote. In (c) conjugation, DNA is transferred from one cell to another via a mating bridge that connects the two cells after the

sex pilus draws the two bacteria close enough to
form the bridge.

land (resistance to drying and the possession of compounds that protect the organism from excess light), photosynthesis using oxygen may be closely linked to adaptations to survive on land.

Section Summary

Prokaryotes (domains Archaea and Bacteria) are single-celled organisms lacking a nucleus. They have a single piece of circular DNA in the nucleoid area of the cell. Most prokaryotes have a cell wall that lies outside the boundary of the plasma membrane. Some prokaryotes may have additional structures such as a capsule, flagella, and pili. Bacteria and Archaea differ in the lipid composition of their cell membranes and the characteristics of the cell wall. In archaeal membranes, phytanyl units, rather than fatty acids, are linked to glycerol. Some archaeal membranes are lipid monolayers instead of bilayers.

The cell wall is located outside the cell membrane and prevents osmotic lysis. The chemical composition of cell walls varies between species. Bacterial cell walls contain peptidoglycan. Archaean cell walls do not have peptidoglycan, but they may have pseudopeptidoglycan, polysaccharides, glycoproteins, or protein-based cell walls. Bacteria can be divided into two major groups: Gram positive and Gram negative, based on the Gram stain reaction. Gram-positive organisms have a thick cell wall, together with teichoic acids. Gram-negative organisms have a thin cell wall and an outer envelope containing lipopolysaccharides and lipoproteins.

Art Connections

Exercise:

Problem: [link] Which of the following statements is true?

 a. Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.

b. Porins allow entry of substances into both Gram-positive and Gram-negative bacteria.
c. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
d. Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.

Solution:

[link] A

Review Questions

Exercise:

Problem:

The presence of a membrane-enclosed nucleus is a characteristic of
_____.

a. prokaryotic cells
b. eukaryotic cells
c. all cells
d. viruses

Solution:

B

Exercise:

Problem: Which of the following consist of prokaryotic cells?

a. bacteria and fungi
b. archaea and fungi

c. protists and animals
d. bacteria and archaea

Solution:

D

Exercise:

Problem: The cell wall is _____.

a. interior to the cell membrane
b. exterior to the cell membrane
c. a part of the cell membrane
d. interior or exterior, depending on the particular cell

Solution:

B

Exercise:

Problem:

Organisms most likely to be found in extreme environments are _____.

a. fungi
b. bacteria
c. viruses
d. archaea

Solution:

B

Exercise:

Problem:

Prokaryotes stain as Gram-positive or Gram-negative because of differences in the cell _____.

    a. wall
    b. cytoplasm
    c. nucleus
    d. chromosome

Solution:

A

Exercise:

Problem:

Pseudopeptidoglycan is a characteristic of the walls of _____.

    a. eukaryotic cells
    b. bacterial prokaryotic cells
    c. archaean prokaryotic cells
    d. bacterial and archaean prokaryotic cells

Solution:

C

Exercise:

Problem:

The lipopolysaccharide layer (LPS) is a characteristic of the wall of _____.

    a. archaean cells
    b. Gram-negative bacteria

c. bacterial prokaryotic cells
d. eukaryotic cells

Solution:

B

Free Response

Exercise:

Problem: Mention three differences between bacteria and archaea.

Solution:

Responses will vary. A possible answer is: Bacteria contain peptidoglycan in the cell wall; archaea do not. The cell membrane in bacteria is a lipid bilayer; in archaea, it can be a lipid bilayer or a monolayer. Bacteria contain fatty acids on the cell membrane, whereas archaea contain phytanyl.

Exercise:

Problem:

Explain the statement that both types, bacteria and archaea, have the same basic structures, but built from different chemical components.

Solution:

Both bacteria and archaea have cell membranes and they both contain a hydrophobic portion. In the case of bacteria, it is a fatty acid; in the case of archaea, it is a hydrocarbon (phytanyl). Both bacteria and archaea have a cell wall that protects them. In the case of bacteria, it is composed of peptidoglycan, whereas in the case of archaea, it is pseudopeptidoglycan, polysaccharides, glycoproteins, or pure protein. Bacterial and archaeal flagella also differ in their chemical structure.

Glossary

capsule
external structure that enables a prokaryote to attach to surfaces and protects it from dehydration

conjugation
process by which prokaryotes move DNA from one individual to another using a pilus

Gram negative
bacterium whose cell wall contains little peptidoglycan but has an outer membrane

Gram positive
bacterium that contains mainly peptidoglycan in its cell walls

peptidoglycan
material composed of polysaccharide chains cross-linked to unusual peptides

pilus
surface appendage of some prokaryotes used for attachment to surfaces including other prokaryotes

pseudopeptidoglycan
component of archaea cell walls that is similar to peptidoglycan in morphology but contains different sugars

S-layer
surface-layer protein present on the outside of cell walls of archaea and bacteria

teichoic acid
polymer associated with the cell wall of Gram-positive bacteria

transduction

process by which a bacteriophage moves DNA from one prokaryote to another

transformation
process by which a prokaryote takes in DNA found in its environment that is shed by other prokaryotes

Prokaryotic Metabolism
By the end of this section, you will be able to:

- Identify the macronutrients needed by prokaryotes, and explain their importance
- Describe the ways in which prokaryotes get energy and carbon for life processes
- Describe the roles of prokaryotes in the carbon and nitrogen cycles

Prokaryotes are metabolically diverse organisms. There are many different environments on Earth with various energy and carbon sources, and variable conditions. Prokaryotes have been able to live in every environment by using whatever energy and carbon sources are available. Prokaryotes fill many niches on Earth, including being involved in nutrient cycles such as nitrogen and carbon cycles, decomposing dead organisms, and thriving inside living organisms, including humans. The very broad range of environments that prokaryotes occupy is possible because they have diverse metabolic processes.

Needs of Prokaryotes

The diverse environments and ecosystems on Earth have a wide range of conditions in terms of temperature, available nutrients, acidity, salinity, and energy sources. Prokaryotes are very well equipped to make their living out of a vast array of nutrients and conditions. To live, prokaryotes need a source of energy, a source of carbon, and some additional nutrients.

Macronutrients

Cells are essentially a well-organized assemblage of macromolecules and water. Recall that macromolecules are produced by the polymerization of smaller units called monomers. For cells to build all of the molecules required to sustain life, they need certain substances, collectively called **nutrients**. When prokaryotes grow in nature, they obtain their nutrients from the environment. Nutrients that are required in large amounts are called macronutrients, whereas those required in smaller or trace amounts are called micronutrients. Just a handful of elements are considered macronutrients—carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur. (A mnemonic for remembering these elements is the acronym *CHONPS*.)

Why are these macronutrients needed in large amounts? They are the components of organic compounds in cells, including water. Carbon is the major element in all macromolecules: carbohydrates, proteins, nucleic acids, lipids, and many other compounds. Carbon accounts for about 50 percent of the composition of the cell. Nitrogen represents 12 percent of the total dry weight of a typical cell and is a component of proteins, nucleic acids, and other cell constituents. Most of the nitrogen available in nature is either atmospheric nitrogen (N_2) or another inorganic form. Diatomic (N_2) nitrogen, however, can be converted into an organic form only by certain organisms, called nitrogen-fixing organisms. Both hydrogen and oxygen are part of many organic compounds and of water. Phosphorus is required by all organisms for the synthesis of nucleotides and phospholipids. Sulfur is part of the structure of some amino acids such as cysteine and methionine, and is also present in several vitamins and

coenzymes. Other important macronutrients are potassium (K), magnesium (Mg), calcium (Ca), and sodium (Na). Although these elements are required in smaller amounts, they are very important for the structure and function of the prokaryotic cell.

Micronutrients

In addition to these macronutrients, prokaryotes require various metallic elements in small amounts. These are referred to as micronutrients or trace elements. For example, iron is necessary for the function of the cytochromes involved in electron-transport reactions. Some prokaryotes require other elements—such as boron (B), chromium (Cr), and manganese (Mn)—primarily as enzyme cofactors.

The Ways in Which Prokaryotes Obtain Energy

Prokaryotes can use different sources of energy to assemble macromolecules from smaller molecules. **Phototrophs** (or phototrophic organisms) obtain their energy from sunlight. **Chemotrophs** (or chemosynthetic organisms) obtain their energy from chemical compounds. Chemotrophs that can use organic compounds as energy sources are called chemoorganotrophs. Those that can also use inorganic compounds as energy sources are called chemolitotrophs.

The Ways in Which Prokaryotes Obtain Carbon

Prokaryotes not only can use different sources of energy but also different sources of carbon compounds. Recall that organisms that are able to fix inorganic carbon are called autotrophs. Autotrophic prokaryotes synthesize organic molecules from carbon dioxide. In contrast, heterotrophic prokaryotes obtain carbon from organic compounds. To make the picture more complex, the terms that describe how prokaryotes obtain energy and carbon can be combined. Thus, photoautotrophs use energy from sunlight, and carbon from carbon dioxide and water, whereas chemoheterotrophs obtain energy and carbon from an organic chemical source. Chemolitoautotrophs obtain their energy from inorganic compounds, and they build their complex molecules from carbon dioxide. The table below ([link]) summarizes carbon and energy sources in prokaryotes.

Carbon and Energy Sources in Prokaryotes

| Carbon and Energy Sources in Prokaryotes | | | Carbon Sources | |

Energy Sources			Carbon Sources	
Light	Chemicals		Carbon dioxide	Organic compounds
Phototrophs	Chemotrophs		Autotrophs	Heterotrophs
	Organic chemicals	Inorganic chemicals		
	Chemo-organotrophs	Chemolithotrophs		

Role of Prokaryotes in Ecosystems

Prokaryotes are ubiquitous: There is no niche or ecosystem in which they are not present. Prokaryotes play many roles in the environments they occupy. The roles they play in the carbon and nitrogen cycles are vital to life on Earth.

Prokaryotes and the Carbon Cycle

Carbon is one of the most important macronutrients, and prokaryotes play an important role in the carbon cycle ([link]). Carbon is cycled through Earth's major reservoirs: land, the atmosphere, aquatic environments, sediments and rocks, and biomass. The movement of carbon is via carbon dioxide, which is removed from the atmosphere by land plants and marine prokaryotes, and is returned to the atmosphere via the respiration of chemoorganotrophic organisms, including prokaryotes, fungi, and animals. Although the largest carbon reservoir in terrestrial ecosystems is in rocks and sediments, that carbon is not readily available.

A large amount of available carbon is found in land plants. Plants, which are producers, use carbon dioxide from the air to synthesize carbon compounds. Related to this, one very significant source of carbon compounds is humus, which is a mixture of organic materials from dead plants and prokaryotes that have resisted decomposition. Consumers such as animals use organic compounds generated by producers and release carbon dioxide to the atmosphere. Then, bacteria and fungi, collectively called **decomposers**, carry out the breakdown (decomposition) of plants and animals and their organic compounds. The most important contributor of carbon dioxide to the atmosphere is microbial decomposition of dead material (dead animals, plants, and humus) that undergo respiration.

In aqueous environments and their anoxic sediments, there is another carbon cycle taking place. In this case, the cycle is based on one-carbon compounds. In anoxic sediments, prokaryotes, mostly archaea, produce methane (CH_4). This methane moves into the zone above the sediment, which is richer in oxygen and supports bacteria called methane oxidizers that oxidize methane to carbon dioxide, which then returns to the atmosphere.
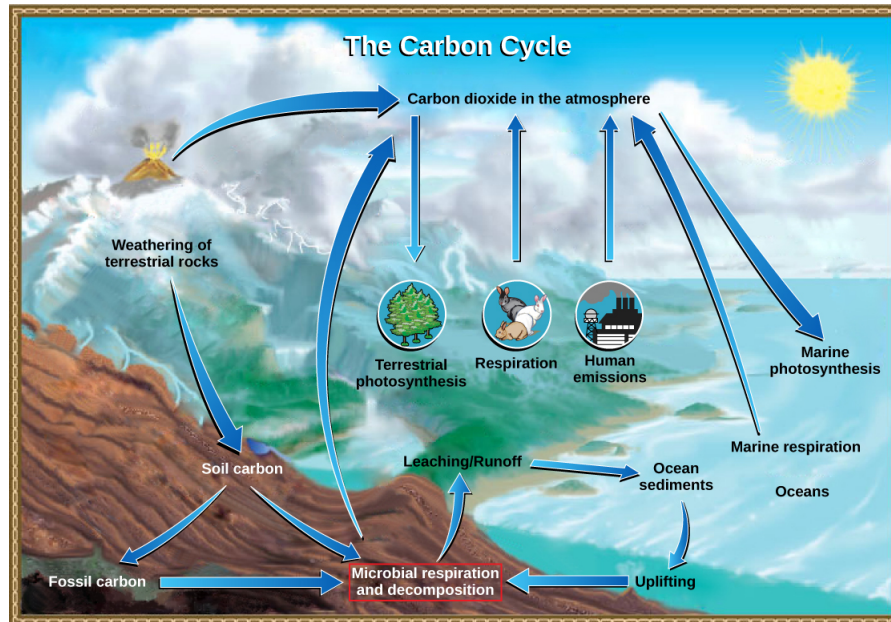
Prokaryotes play a significant role in continuously moving carbon through the biosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Prokaryotes and the Nitrogen Cycle

Nitrogen is a very important element for life because it is part of proteins and nucleic acids. It is a macronutrient, and in nature, it is recycled from organic compounds to ammonia, ammonium ions, nitrate, nitrite, and nitrogen gas by myriad processes, many of which are carried out only by prokaryotes. As illustrated in [link], prokaryotes are key to the nitrogen cycle. The largest pool of nitrogen available in the terrestrial ecosystem is gaseous nitrogen from the air, but this nitrogen is not usable by plants, which are primary producers. Gaseous nitrogen is transformed, or "fixed" into more readily available forms such as ammonia through the process of **nitrogen fixation**. Ammonia can be used by plants or converted to other forms.

Another source of ammonia is **ammonification**, the process by which ammonia is released during the decomposition of nitrogen-containing organic compounds. Ammonia released to the atmosphere, however, represents only 15 percent of the total nitrogen released; the rest is as N_2 and N_2O. Ammonia is catabolized anaerobically by some prokaryotes, yielding N_2 as the final product. **Nitrification** is the conversion of ammonium to nitrite and nitrate. Nitrification in soils is carried out by bacteria belonging to the genera *Nitrosomas*, *Nitrobacter*, and *Nitrospira*. The bacteria performs the reverse process, the reduction of nitrate from the soils to gaseous compounds such as N_2O, NO, and N_2, a process called **denitrification**.

Note:
Art Connection
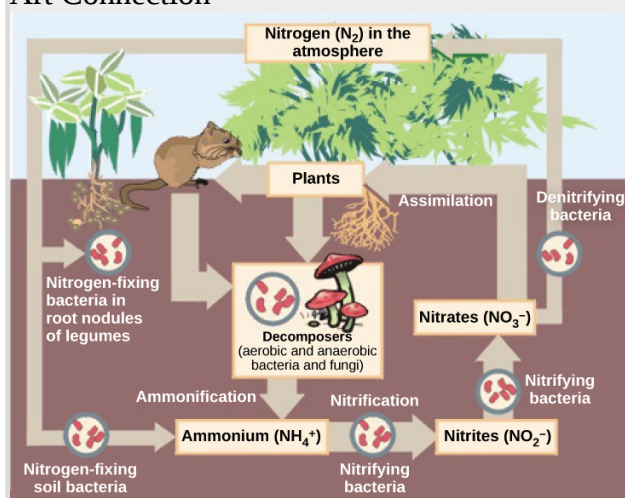
Prokaryotes play a key role in the nitrogen cycle. (credit: Environmental Protection Agency)

Which of the following statements about the nitrogen cycle is false?

a. Nitrogen fixing bacteria exist on the root nodules of legumes and in the soil.
b. Denitrifying bacteria convert nitrates (NO_3^-) into nitrogen gas (N_2).
c. Ammonification is the process by which ammonium ion (NH_4^+) is released from decomposing organic compounds.
d. Nitrification is the process by which nitrites (NO_2^-) are converted to ammonium ion (NH_4^+).

Section Summary

Prokaryotes are the most metabolically diverse organisms; they flourish in many different environments with various carbon energy and carbon sources, variable temperature, pH, pressure, and water availability. Nutrients required in large amounts are called macronutrients, whereas those required in trace amounts are called micronutrients or trace elements. Macronutrients include C, H, O, N, P, S, K, Mg, Ca, and Na. In addition to these macronutrients, prokaryotes require various metallic elements for growth and enzyme function. Prokaryotes use different sources of energy to assemble macromolecules from smaller molecules. Phototrophs obtain their energy from sunlight, whereas chemotrophs obtain energy from chemical compounds.

Prokaryotes play roles in the carbon and nitrogen cycles. Carbon is returned to the atmosphere by the respiration of animals and other chemoorganotrophic organisms. Consumers use organic compounds generated by producers and release carbon dioxide into the atmosphere. The most important contributor of carbon dioxide to the atmosphere is microbial decomposition of dead material. Nitrogen is recycled in nature from organic compounds to ammonia, ammonium ions, nitrite, nitrate, and nitrogen gas. Gaseous nitrogen is transformed into ammonia through nitrogen fixation. Ammonia is anaerobically catabolized by some prokaryotes, yielding N_2 as the final product. Nitrification is the conversion of ammonium into nitrite. Nitrification in soils is carried out by bacteria. Denitrification is also performed by bacteria and transforms nitrate from soils into gaseous nitrogen compounds, such as N_2O, NO, and N_2.

Art Connections

Exercise:

Problem: [link] Which of the following statements about the nitrogen cycle is false?

- a. Nitrogen fixing bacteria exist on the root nodules of legumes and in the soil.
- b. Denitrifying bacteria convert nitrates (NO_3^-) into nitrogen gas (N_2).
- c. Ammonification is the process by which ammonium ion (NH_4^+) is released from decomposing organic compounds.
- d. Nitrification is the process by which nitrites (NO_2^-) are converted to ammonium ion (NH_4^+).

Solution:

[link] D

Review Questions

Exercise:

Problem: Which of the following elements is *not* a micronutrient?

a. boron
b. calcium
c. chromium
d. manganese

Solution:

B

Exercise:

Problem:

Prokaryotes that obtain their energy from chemical compounds are called _____.

a. phototrophs
b. auxotrophs
c. chemotrophs
d. lithotrophs

Solution:

C

Exercise:

Problem: Ammonification is the process by which _____.

a. ammonia is released during the decomposition of nitrogen-containing organic compounds
b. ammonium is converted to nitrite and nitrate in soils
c. nitrate from soil is transformed to gaseous nitrogen compounds such as NO, N_2O, and N_2
d. gaseous nitrogen is fixed to yield ammonia

Solution:

A

Exercise:

Problem: Plants use carbon dioxide from the air and are therefore called _____.

a. consumers
b. producers
c. decomposer

d. carbon fixers

Solution:

B

Free Response

Exercise:

Problem:

Think about the conditions (temperature, light, pressure, and organic and inorganic materials) that you may find in a deep-sea hydrothermal vent. What type of prokaryotes, in terms of their metabolic needs (autotrophs, phototrophs, chemotrophs, etc.), would you expect to find there?

Solution:

Responses will vary. In a deep-sea hydrothermal vent, there is no light, so prokaryotes would be chemotrophs instead of phototrophs. The source of carbon would be carbon dioxide dissolved in the ocean, so they would be autotrophs. There is not a lot of organic material in the ocean, so prokaryotes would probably use inorganic sources, thus they would be chemolitotrophs. The temperatures are very high in the hydrothermal vent, so the prokaryotes would be thermophilic.

Glossary

ammonification
  process by which ammonia is released during the decomposition of nitrogen-containing organic compounds

chemotroph
  organism that obtains energy from chemical compounds

decomposer
  organism that carries out the decomposition of dead organisms

denitrification
  transformation of nitrate from soil to gaseous nitrogen compounds such as N_2O, NO and N_2

nitrification
  conversion of ammonium into nitrite and nitrate in soils

nitrogen fixation
    process by which gaseous nitrogen is transformed, or "fixed" into more readily available
    forms such as ammonia

Bacterial Diseases in Humans
By the end of this section, you will be able to:

- Identify bacterial diseases that caused historically important plagues and epidemics
- Describe the link between biofilms and foodborne diseases
- Explain how overuse of antibiotic may be creating "super bugs"
- Explain the importance of MRSA with respect to the problems of antibiotic resistance

Devastating pathogen-borne diseases and plagues, both viral and bacterial in nature, have affected humans since the beginning of human history. The true cause of these diseases was not understood at the time, and some people thought that diseases were a spiritual punishment. Over time, people came to realize that staying apart from afflicted persons, and disposing of the corpses and personal belongings of victims of illness, reduced their own chances of getting sick.

Epidemiologists study how diseases affect a population. An **epidemic** is a disease that occurs in an unusually high number of individuals in a population at the same time. A **pandemic** is a widespread, usually worldwide, epidemic. An **endemic disease** is a disease that is constantly present, usually at low incidence, in a population.

Long History of Bacterial Disease

There are records about infectious diseases as far back as 3000 B.C. A number of significant pandemics caused by bacteria have been documented over several hundred years. Some of the most memorable pandemics led to the decline of cities and nations.

In the 21st century, infectious diseases remain among the leading causes of death worldwide, despite advances made in medical research and treatments in recent decades. A disease spreads when the pathogen that causes it is passed from one person to another. For a pathogen to cause disease, it must be able to reproduce in the host's body and damage the host in some way.

The Plague of Athens

In 430 B.C., the Plague of Athens killed one-quarter of the Athenian troops that were fighting in the great Peloponnesian War and weakened Athens' dominance and power. The plague impacted people living in overcrowded Athens as well as troops aboard ships that had to return to Athens. The source of the plague may have been identified recently when researchers from the University of Athens were able to use DNA from teeth recovered from a mass grave. The scientists identified nucleotide sequences from a pathogenic bacterium, *Salmonella enterica* serovar Typhi ([link]), which causes typhoid fever.[footnote] This disease is commonly seen in overcrowded areas and has caused epidemics throughout recorded history. Papagrigorakis MJ, Synodinos PN, and Yapijakis C. Ancient typhoid epidemic reveals possible ancestral strain of *Salmonella enterica* serovar Typhi. *Infect Genet Evol* 7 (2007): 126–7, Epub 2006 Jun.

Salmonella enterica serovar Typhi, the causative agent of Typhoid fever, is a Gram-negative, rod-shaped gamma protobacterium. Typhoid fever, which is spread through feces, causes intestinal hemorrhage, high fever, delirium and dehydration. Today, between 16 and 33 million

cases of this re-emerging disease occur annually, resulting in over 200,000 deaths. Carriers of the disease can be asymptomatic. In a famous case in the early 1900s, a cook named Mary Mallon unknowingly spread the disease to over fifty people, three of whom died. Other *Salmonella* serotypes cause food poisoning. (credit: modification of work by NCI, CDC)

Bubonic Plagues

From 541 to 750, an outbreak of what was likely a bubonic plague (the Plague of Justinian), eliminated one-quarter to one-half of the human population in the eastern Mediterranean region. The population in Europe dropped by 50 percent during this outbreak. Bubonic plague would strike Europe more than once.

One of the most devastating pandemics was the **Black Death** (1346 to 1361) that is believed to have been another outbreak of bubonic plague caused by the bacterium *Yersinia pestis*. It is thought to have originated initially in China and spread along the Silk Road, a network of land and sea trade routes, to the Mediterranean region and Europe, carried by rat fleas living on black rats that were always present on ships. The Black Death reduced the world's population from an estimated 450 million to about 350 to 375 million. Bubonic plague struck London hard again in the mid-1600s ([link]). In modern times, approximately 1,000 to 3,000 cases of plague arise globally each year. Although contracting bubonic plague before antibiotics meant almost certain death, the bacterium responds to several types of modern antibiotics, and mortality rates from plague are now very low.
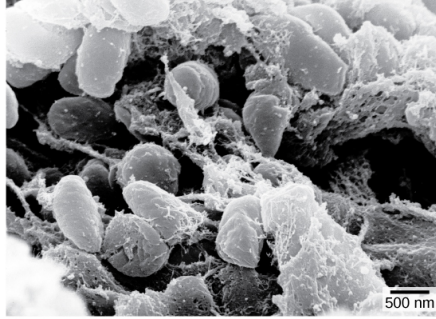
The (a) Great Plague of London killed an estimated 200,000 people, or about twenty percent of the city's population. The causative agent, the (b) bacterium *Yersinia pestis*, is a Gram-negative, rod-shaped bacterium from the class Gamma Proteobacteria. The disease is transmitted through the bite of an infected flea, which is infected by a rodent. Symptoms include swollen lymph nodes, fever, seizure, vomiting of blood, and (c) gangrene. (credit b: Rocky Mountain Laboratories, NIAID, NIH; scale-bar data from Matt Russell; credit c: Textbook of Military Medicine, Washington, D.C., U.S. Dept. of the Army, Office of the Surgeon General, Borden Institute)

Note:
Link to Learning

Watch a [video](#) on the modern understanding of the Black Death—bubonic plague in Europe during the 14th century.

Migration of Diseases to New Populations

Over the centuries, Europeans tended to develop genetic immunity to endemic infectious diseases, but when European conquerors reached the western hemisphere, they brought with them disease-causing bacteria and viruses, which triggered epidemics that completely devastated populations of Native Americans, who had no natural resistance to many European diseases. It has been estimated that up to 90 percent of Native Americans died from infectious diseases after the arrival of Europeans, making conquest of the New World a foregone conclusion.

Emerging and Re-emerging Diseases

The distribution of a particular disease is dynamic. Therefore, changes in the environment, the pathogen, or the host population can dramatically impact the spread of a disease. According to the World Health Organization (WHO) an **emerging disease** ([link]) is one that has appeared in a population for the first time, or that may have existed previously but is rapidly increasing in incidence or geographic range. This definition also includes re-emerging diseases that were previously under control. Approximately 75 percent of recently emerging infectious diseases affecting humans are zoonotic diseases, **zoonoses**, diseases that primarily infect animals and are transmitted to humans; some are of viral origin and some are of bacterial origin. Brucellosis is an example of a prokaryotic zoonosis that is re-emerging in some regions, and necrotizing fasciitis (commonly known as flesh-eating bacteria) has been increasing in virulence for the last 80 years for unknown reasons.
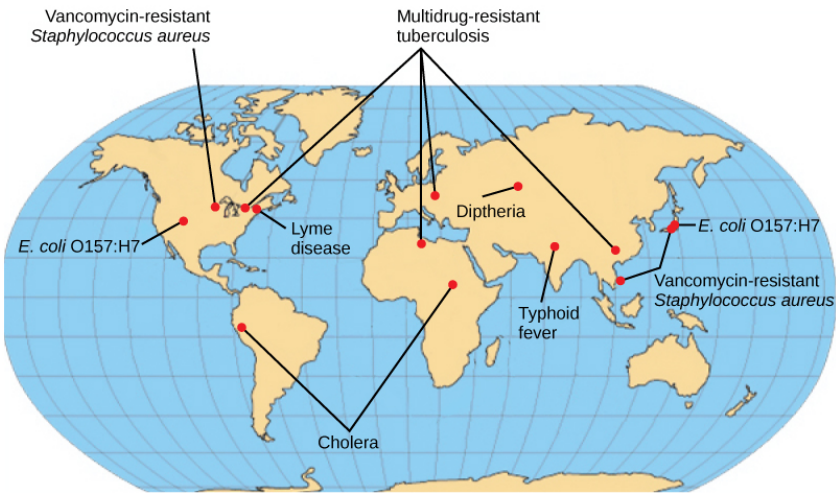
The map shows regions where bacterial diseases are emerging or reemerging. (credit: modification of work by NIH)

Some of the present emerging diseases are not actually new, but are diseases that were catastrophic in the past ([link]). They devastated populations and became dormant for a while, just to come back, sometimes more virulent than before, as was the case with bubonic plague. Other diseases, like tuberculosis, were never eradicated but were under control in some regions of the world until coming back, mostly in urban centers with high concentrations of immunocompromised people. The WHO has identified certain diseases whose worldwide re-emergence should be monitored. Among these are two viral diseases (dengue fever and yellow fever), and three bacterial diseases (diphtheria, cholera, and bubonic plague). The war against infectious diseases has no foreseeable end.

Life Cycle of the *Ixodes scapularis* Tick
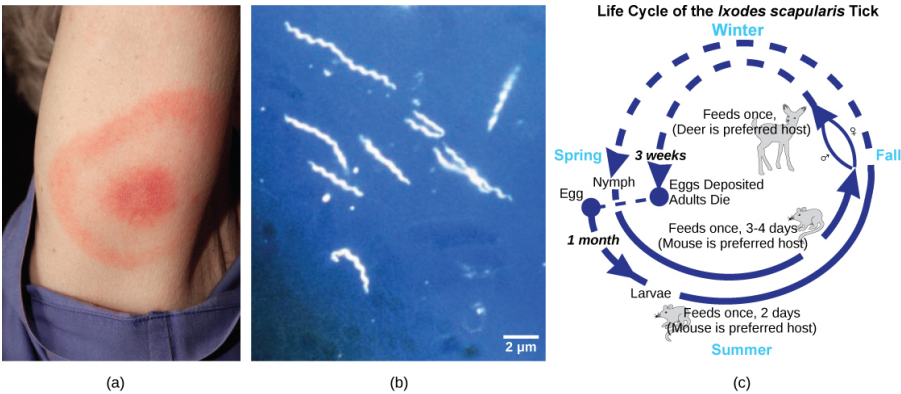
Lyme disease often, but not always, results in (a) a characteristic bullseye rash. The disease is caused by a (b) Gram-negative spirochete bacterium of the genus *Borrelia*. The bacteria (c) infect ticks, which in turns infect mice. Deer are the preferred secondary host, but the ticks also may feed on humans. Untreated, the disease causes chronic disorders in the nervous system, eyes, joints, and heart. The disease is named after Lyme, Connecticut, where an outbreak occurred in 1995 and has subsequently spread. The disease is not new, however. Genetic evidence suggests that Ötzi the Iceman, a 5,300-year-old mummy found in the Alps, was infected with *Borrelia*. (credit a: James Gathany, CDC; credit b: CDC; scale-bar data from Matt Russell)

Biofilms and Disease

Recall that biofilms are microbial communities that are very difficult to destroy. They are responsible for diseases such as infections in patients with cystic fibrosis, Legionnaires' disease, and otitis media. They produce dental plaque and colonize catheters, prostheses, transcutaneous and orthopedic devices, contact lenses, and internal devices such as pacemakers. They also form in open wounds and burned tissue. In healthcare environments,

biofilms grow on hemodialysis machines, mechanical ventilators, shunts, and other medical equipment. In fact, 65 percent of all infections acquired in the hospital (nosocomial infections) are attributed to biofilms. Biofilms are also related to diseases contracted from food because they colonize the surfaces of vegetable leaves and meat, as well as food-processing equipment that isn't adequately cleaned.

Biofilm infections develop gradually; sometimes, they do not cause symptoms immediately. They are rarely resolved by host defense mechanisms. Once an infection by a biofilm is established, it is very difficult to eradicate, because biofilms tend to be resistant to most of the methods used to control microbial growth, including antibiotics. Biofilms respond poorly or only temporarily to antibiotics; it has been said that they can resist up to 1,000 times the antibiotic concentrations used to kill the same bacteria when they are free-living or planktonic. An antibiotic dose that large would harm the patient; therefore, scientists are working on new ways to get rid of biofilms.

Antibiotics: Are We Facing a Crisis?

The word *antibiotic* comes from the Greek *anti* meaning "against" and *bios* meaning "life." An **antibiotic** is a chemical, produced either by microbes or synthetically, that is hostile to the growth of other organisms. Today's news and media often address concerns about an antibiotic crisis. Are the antibiotics that easily treated bacterial infections in the past becoming obsolete? Are there new "superbugs"—bacteria that have evolved to become more resistant to our arsenal of antibiotics? Is this the beginning of the end of antibiotics? All these questions challenge the healthcare community.

One of the main causes of resistant bacteria is the abuse of antibiotics. The imprudent and excessive use of antibiotics has resulted in the natural selection of resistant forms of bacteria. The antibiotic kills most of the infecting bacteria, and therefore only the resistant forms remain. These resistant forms reproduce, resulting in an increase in the proportion of resistant forms over non-resistant ones. Another major misuse of antibiotics is in patients with colds or the flu, for which antibiotics are useless. Another

problem is the excessive use of antibiotics in livestock. The routine use of antibiotics in animal feed promotes bacterial resistance as well. In the United States, 70 percent of the antibiotics produced are fed to animals. These antibiotics are given to livestock in low doses, which maximize the probability of resistance developing, and these resistant bacteria are readily transferred to humans.

One of the Superbugs: MRSA

The imprudent use of antibiotics has paved the way for bacteria to expand populations of resistant forms. For example, *Staphylococcus aureu*s, often called "staph," is a common bacterium that can live in the human body and is usually easily treated with antibiotics. A very dangerous strain, however, **methicillin-resistant *Staphylococcus aureus* (MRSA)** has made the news over the past few years ([link]). This strain is resistant to many commonly used antibiotics, including methicillin, amoxicillin, penicillin, and oxacillin. MRSA can cause infections of the skin, but it can also infect the bloodstream, lungs, urinary tract, or sites of injury. While MRSA infections are common among people in healthcare facilities, they have also appeared in healthy people who haven't been hospitalized but who live or work in tight populations (like military personnel and prisoners). Researchers have expressed concern about the way this latter source of MRSA targets a much

younger population than those residing in care facilities. *The Journal of the American Medical Association* reported that, among MRSA-afflicted persons in healthcare facilities, the average age is 68, whereas people with "community-associated MRSA" (**CA-MRSA**) have an average age of 23.
[footnote]
Naimi, TS, LeDell, KH, Como-Sabetti, K, et al. Comparison of community- and health care-associated methicillin-resistant *Staphylococcus aureus* infection. *JAMA* 290 (2003): 2976–84, doi: 10.1001/jama.290.22.2976.
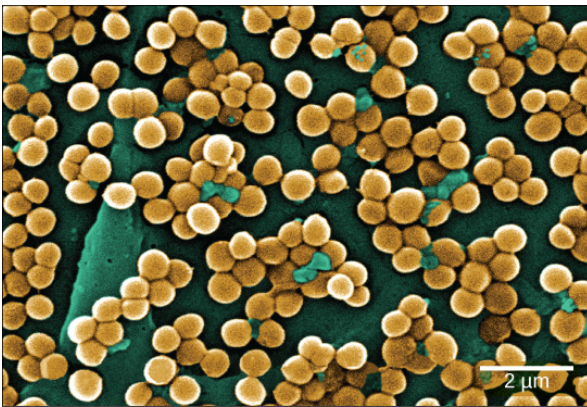
This scanning electron micrograph shows methicillin-resistant *Staphylococcus aureus* bacteria, commonly known as MRSA. *S. aureus* is not always pathogenic, but can cause diseases such as food poisoning and skin and respiratory infections. (credit: modification of work by Janice Haney Carr; scale-bar data from Matt Russell)

In summary, the medical community is facing an antibiotic crisis. Some scientists believe that after years of being protected from bacterial

infections by antibiotics, we may be returning to a time in which a simple bacterial infection could again devastate the human population. Researchers are developing new antibiotics, but it takes many years to of research and clinical trials, plus financial investments in the millions of dollars, to generate an effective and approved drug.

Foodborne Diseases

Prokaryotes are everywhere: They readily colonize the surface of any type of material, and food is not an exception. Most of the time, prokaryotes colonize food and food-processing equipment in the form of a biofilm. Outbreaks of bacterial infection related to food consumption are common. A **foodborne disease** (colloquially called "food poisoning") is an illness resulting from the consumption the pathogenic bacteria, viruses, or other parasites that contaminate food. Although the United States has one of the safest food supplies in the world, the U.S. Centers for Disease Control and Prevention (CDC) has reported that "76 million people get sick, more than 300,000 are hospitalized, and 5,000 Americans die each year from foodborne illness."

The characteristics of foodborne illnesses have changed over time. In the past, it was relatively common to hear about sporadic cases of **botulism**, the potentially fatal disease produced by a toxin from the anaerobic bacterium *Clostridium botulinum*. Some of the most common sources for this bacterium were non-acidic canned foods, homemade pickles, and processed meat and sausages. The can, jar, or package created a suitable anaerobic environment where *Clostridium* could grow. Proper sterilization and canning procedures have reduced the incidence of this disease.

While people may tend to think of foodborne illnesses as associated with animal-based foods, most cases are now linked to produce. There have been serious, produce-related outbreaks associated with raw spinach in the United States and with vegetable sprouts in Germany, and these types of outbreaks have become more common. The raw spinach outbreak in 2006 was produced by the bacterium *E. coli* serotype O157:H7. A **serotype** is a strain of bacteria that carries a set of similar antigens on its cell surface, and there are often many different serotypes of a bacterial species. Most *E. coli*

are not particularly dangerous to humans, but serotype O157:H7 can cause bloody diarrhea and is potentially fatal.

All types of food can potentially be contaminated with bacteria. Recent outbreaks of *Salmonella* reported by the CDC occurred in foods as diverse as peanut butter, alfalfa sprouts, and eggs. A deadly outbreak in Germany in 2010 was caused by *E. coli* contamination of vegetable sprouts ([link]). The strain that caused the outbreak was found to be a new serotype not previously involved in other outbreaks, which indicates that *E. coli* is continuously evolving.

(a)   (b)   (c)
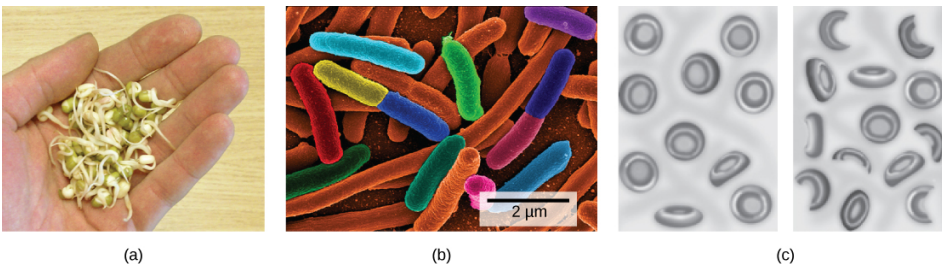
(a) Vegetable sprouts grown at an organic farm were the cause of an (b) *E. coli* outbreak that killed 32 people and sickened 3,800 in Germany in 2011. The strain responsible, *E. coli* O104:H4, produces Shiga toxin, a substance that inhibits protein synthesis in the host cell. The toxin (c) destroys red blood cells resulting in bloody diarrhea. Deformed red blood cells clog the capillaries of the kidney, which can lead to kidney failure, as happened to 845 patients in the 2011 outbreak. Kidney failure is usually reversible, but some patients experience kidney problems years later. (credit c: NIDDK, NIH)

Note:

Career Connection

Epidemiologist

Epidemiology is the study of the occurrence, distribution, and determinants of health and disease in a population. It is, therefore, part of public health. An epidemiologist studies the frequency and distribution of diseases within human populations and environments.

Epidemiologists collect data about a particular disease and track its spread to identify the original mode of transmission. They sometimes work in close collaboration with historians to try to understand the way a disease evolved geographically and over time, tracking the natural history of pathogens. They gather information from clinical records, patient interviews, surveillance, and any other available means. That information is used to develop strategies, such as vaccinations ([link]), and design public health policies to reduce the incidence of a disease or to prevent its spread. Epidemiologists also conduct rapid investigations in case of an outbreak to recommend immediate measures to control it.

An epidemiologist has a bachelor's degree, plus a master's degree in public health (MPH). Many epidemiologists are also physicians (and have an M.D.), or they have a Ph.D. in an associated field, such as biology or microbiology.

Vaccinations can slow the spread of communicable diseases. (credit: modification of work by Daniel Paquet)

Section Summary

Devastating diseases and plagues have been among us since early times. There are records about microbial diseases as far back as 3000 B.C. Infectious diseases remain among the leading causes of death worldwide. Emerging diseases are those rapidly increasing in incidence or geographic range. They can be new or re-emerging diseases (previously under control). Many emerging diseases affecting humans, such as brucellosis, are zoonoses. The WHO has identified a group of diseases whose re-emergence should be monitored: Those caused by bacteria include bubonic plague, diphtheria, and cholera.

Biofilms are considered responsible for diseases such as bacterial infections in patients with cystic fibrosis, Legionnaires' disease, and otitis media. They produce dental plaque; colonize catheters, prostheses, transcutaneous, and orthopedic devices; and infect contact lenses, open wounds, and burned tissue. Biofilms also produce foodborne diseases because they colonize the surfaces of food and food-processing equipment. Biofilms are resistant to most of the methods used to control microbial growth. The excessive use of antibiotics has resulted in a major global problem, since resistant forms of bacteria have been selected over time. A very dangerous strain, methicillin-resistant *Staphylococcus aureus* (MRSA), has wreaked havoc recently. Foodborne diseases result from the consumption of contaminated food, pathogenic bacteria, viruses, or parasites that contaminate food.

Review Questions

Exercise:

  Problem:

  A disease that is constantly present in a population is called _____.

      a. pandemic
      b. epidemic
      c. endemic
      d. re-emerging

Solution:

C

Exercise:

Problem: Which of the statements about biofilms is incorrect?

a. Biofilms are considered responsible for diseases such as cystic fibrosis.
b. Biofilms produce dental plaque, and colonize catheters and prostheses.
c. Biofilms colonize open wounds and burned tissue.
d. All statements are incorrect.

Solution:

D

Exercise:

Problem: Which of these statements is true?

a. An antibiotic is any substance produced by a organism that is antagonistic to the growth of prokaryotes.
b. An antibiotic is any substance produced by a prokaryote that is antagonistic to the growth of other viruses.
c. An antibiotic is any substance produced by a prokaryote that is antagonistic to the growth of eukaryotic cells.
d. An antibiotic is any substance produced by a prokaryote that prevents growth of the same prokaryote.

Solution:

A

Free Response

Exercise:

Problem:

Explain the reason why the imprudent and excessive use of antibiotics has resulted in a major global problem.

Solution:

Antibiotics kill bacteria that are sensitive to them; thus, only the resistant ones will survive. These resistant bacteria will reproduce, and therefore, after a while, there will be only resistant bacteria.

Exercise:

Problem:

Researchers have discovered that washing spinach with water several times does not prevent foodborne diseases due to *E. coli*. How can you explain this fact?

Solution:

E. coli colonizes the surface of the leaf, forming a biofilm that is more difficult to remove than free (planktonic) cells. Additionally, bacteria can be taken up in the water that plants are grown in, thereby entering the plant tissues rather than simply residing on the leaf surface.

Glossary

antibiotic
> biological substance that, in low concentration, is antagonistic to the growth of prokaryotes

Black Death
> devastating pandemic that is believed to have been an outbreak of bubonic plague caused by the bacterium *Yersinia pestis*

botulism
   disease produced by the toxin of the anaerobic bacterium *Clostridium botulinum*

CA-MRSA
   MRSA acquired in the community rather than in a hospital setting

emerging disease
   disease making an initial appearance in a population or that is increasing in incidence or geographic range

endemic disease
   disease that is constantly present, usually at low incidence, in a population

epidemic
   disease that occurs in an unusually high number of individuals in a population at the same time

foodborne disease
   any illness resulting from the consumption of contaminated food, or of the pathogenic bacteria, viruses, or other parasites that contaminate food

MRSA
   (methicillin-resistant *Staphylococcus aureus*) very dangerous *Staphylococcus aureus* strain resistant to multiple antibiotics

pandemic
   widespread, usually worldwide, epidemic disease

serotype
   strain of bacteria that carries a set of similar antigens on its cell surface, often many in a bacterial species

zoonosis
   disease that primarily infects animals that is transmitted to humans

Beneficial Prokaryotes
By the end of this section, you will be able to:

- Explain the need for nitrogen fixation and how it is accomplished
- Identify foods in which prokaryotes are used in the processing
- Describe the use of prokaryotes in bioremediation
- Describe the beneficial effects of bacteria that colonize our skin and digestive tracts

Not all prokaryotes are pathogenic. On the contrary, pathogens represent only a very small percentage of the diversity of the microbial world. In fact, our life would not be possible without prokaryotes. Just think about the role of prokaryotes in biogeochemical cycles.

Cooperation between Bacteria and Eukaryotes: Nitrogen Fixation

Nitrogen is a very important element to living things, because it is part of nucleotides and amino acids that are the building blocks of nucleic acids and proteins, respectively. Nitrogen is usually the most limiting element in terrestrial ecosystems, with atmospheric nitrogen, N_2, providing the largest pool of available nitrogen. However, eukaryotes cannot use atmospheric, gaseous nitrogen to synthesize macromolecules. Fortunately, nitrogen can be "fixed," meaning it is converted into ammonia (NH_3) either biologically or abiotically. Abiotic nitrogen fixation occurs as a result of lightning or by industrial processes.

Biological nitrogen fixation (BNF) is exclusively carried out by prokaryotes: soil bacteria, cyanobacteria, and *Frankia* spp. (filamentous bacteria interacting with actinorhizal plants such as alder, bayberry, and sweet fern). After photosynthesis, BNF is the second most important biological process on Earth. The equation representing the process is as follows
Equation:

$$N_2 + 16ATP + 8e^- + 8H^+ \rightarrow 2NH_3 + 16ADP + 16Pi + H_2$$
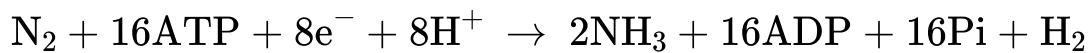
where Pi stands for inorganic phosphate. The total fixed nitrogen through BNF is about 100 to 180 million metric tons per year. Biological processes contribute 65 percent of the nitrogen used in agriculture.

Cyanobacteria are the most important nitrogen fixers in aquatic environments. In soil, members of the genus *Clostridium* are examples of free-living, nitrogen-fixing bacteria. Other bacteria live symbiotically with legume plants, providing the most important source of BNF. Symbionts may fix more nitrogen in soils than free-living organisms by a factor of 10. Soil bacteria, collectively called rhizobia, are able to symbiotically interact with legumes to form **nodules**, specialized structures where nitrogen fixation occurs ([link]). Nitrogenase, the enzyme that fixes nitrogen, is inactivated by oxygen, so the nodule provides an oxygen-free area for nitrogen fixation to take place. This process provides a natural and inexpensive plant fertilizer, as it reduces atmospheric nitrogen to ammonia, which is easily usable by plants. The use of legumes is an excellent alternative to chemical fertilization and is of special interest to sustainable agriculture, which seeks to minimize the use of chemicals and conserve natural resources. Through symbiotic nitrogen fixation, the plant benefits from using an endless source of nitrogen: the atmosphere. Bacteria benefit from using photosynthates (carbohydrates produced during photosynthesis) from the plant and having a protected niche. Additionally, the soil benefits from being naturally fertilized. Therefore, the use of rhizobia as biofertilizers is a sustainable practice.

Why are legumes so important? Some, like soybeans, are key sources of agricultural protein. Some of the most important grain legumes are soybean, peanuts, peas, chickpeas, and beans. Other legumes, such as alfalfa, are used to feed cattle.

Soybean (*Glycine max*) is a legume that interacts symbiotically with the soil bacterium *Bradyrhizobium japonicum* to form specialized structures on the roots called nodules where nitrogen fixation occurs. (credit: USDA)

Early Biotechnology: Cheese, Bread, Wine, Beer, and Yogurt

According to the United Nations Convention on Biological Diversity, **biotechnology** is "any technological application that uses biological systems, living organisms, or derivatives thereof, to make or modify products or processes for specific use."[footnote] The concept of "specific use" involves some sort of commercial application. Genetic engineering, artificial selection, antibiotic production, and cell culture are current topics of study in biotechnology. However, humans have used prokaryotes before the term biotechnology was even coined. In addition, some of the goods and services are as simple as cheese, bread, wine, beer, and yogurt, which employ both bacteria and other microbes, such as yeast, a fungus ([link]). http://www.cbd.int/convention/articles/?a=cbd-02, United Nations Convention on Biological Diversity: Article 2: Use of Terms.

Some of the products derived from the use of prokaryotes in early biotechnology include (a) cheese, (b) wine, (c) beer and bread, and (d) yogurt. (credit bread: modification of work by F. Rodrigo/Wikimedia Commons; credit wine: modification of work by Jon Sullivan; credit beer and bread: modification of work by Kris Miller; credit yogurt: modification of work by Jon Sullivan)

Cheese production began around 4,000–7,000 years ago when humans began to breed animals and process their milk. Fermentation in this case preserves nutrients: Milk will spoil relatively quickly, but when processed as cheese, it is more stable. As for beer, the oldest records of brewing are about 6,000 years old and refer to the Sumerians. Evidence indicates that the Sumerians discovered fermentation by chance. Wine has been produced

for about 4,500 years, and evidence suggests that cultured milk products, like yogurt, have existed for at least 4,000 years.

Using Prokaryotes to Clean up Our Planet: Bioremediation

Microbial **bioremediation** is the use of prokaryotes (or microbial metabolism) to remove pollutants. Bioremediation has been used to remove agricultural chemicals (pesticides, fertilizers) that leach from soil into groundwater and the subsurface. Certain toxic metals and oxides, such as selenium and arsenic compounds, can also be removed from water by bioremediation. The reduction of SeO_4^{-2} to SeO_3^{-2} and to Se^0 (metallic selenium) is a method used to remove selenium ions from water. Mercury is an example of a toxic metal that can be removed from an environment by bioremediation. As an active ingredient of some pesticides, mercury is used in industry and is also a by-product of certain processes, such as battery production. Methyl mercury is usually present in very low concentrations in natural environments, but it is highly toxic because it accumulates in living tissues. Several species of bacteria can carry out the biotransformation of toxic mercury into nontoxic forms. These bacteria, such as *Pseudomonas aeruginosa*, can convert Hg^{+2} into Hg^0, which is nontoxic to humans.

One of the most useful and interesting examples of the use of prokaryotes for bioremediation purposes is the cleanup of oil spills. The importance of prokaryotes to petroleum bioremediation has been demonstrated in several oil spills in recent years, such as the Exxon Valdez spill in Alaska (1989) ([link]), the Prestige oil spill in Spain (2002), the spill into the Mediterranean from a Lebanon power plant (2006), and more recently, the BP oil spill in the Gulf of Mexico (2010). To clean up these spills, bioremediation is promoted by the addition of inorganic nutrients that help bacteria to grow. Hydrocarbon-degrading bacteria feed on hydrocarbons in the oil droplet, breaking down the hydrocarbons. Some species, such as *Alcanivorax borkumensis*, produce surfactants that solubilize the oil, whereas other bacteria degrade the oil into carbon dioxide. In the case of oil spills in the ocean, ongoing, natural bioremediation tends to occur, inasmuch as there are oil-consuming bacteria in the ocean prior to the spill. In addition to naturally occurring oil-degrading bacteria, humans select and engineer bacteria that possess the same capability with increased efficacy

and spectrum of hydrocarbon compounds that can be processed. Under ideal conditions, it has been reported that up to 80 percent of the nonvolatile components in oil can be degraded within one year of the spill. Other oil fractions containing aromatic and highly branched hydrocarbon chains are more difficult to remove and remain in the environment for longer periods of time.
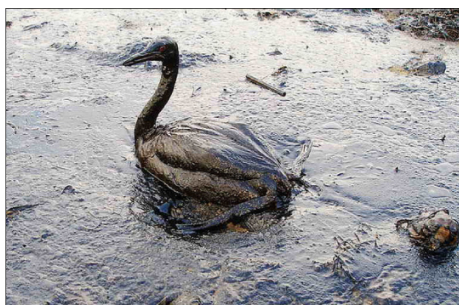
(a) Cleaning up oil after the Valdez spill in Alaska, workers hosed oil from beaches and then used a floating boom to corral the oil, which was finally skimmed from the water surface. Some species of bacteria are able to solubilize and degrade the oil. (b) One of the most catastrophic consequences of oil spills is the damage to fauna. (credit a: modification of work by NOAA; credit b: modification of work by GOLUBENKOV, NGO: Saving Taman)

Note:
Everyday Connection
Microbes on the Human Body
The commensal bacteria that inhabit our skin and gastrointestinal tract do a host of good things for us. They protect us from pathogens, help us digest our food, and produce some of our vitamins and other nutrients. These

activities have been known for a long time. More recently, scientists have gathered evidence that these bacteria may also help regulate our moods, influence our activity levels, and even help control weight by affecting our food choices and absorption patterns. The Human Microbiome Project has begun the process of cataloging our normal bacteria (and archaea) so we can better understand these functions.

A particularly fascinating example of our normal flora relates to our digestive systems. People who take high doses of antibiotics tend to lose many of their normal gut bacteria, allowing a naturally antibiotic-resistant species called *Clostridium difficile* to overgrow and cause severe gastric problems, especially chronic diarrhea ([link]). Obviously, trying to treat this problem with antibiotics only makes it worse. However, it has been successfully treated by giving the patients fecal transplants from healthy donors to reestablish the normal intestinal microbial community. Clinical trials are underway to ensure the safety and effectiveness of this technique.
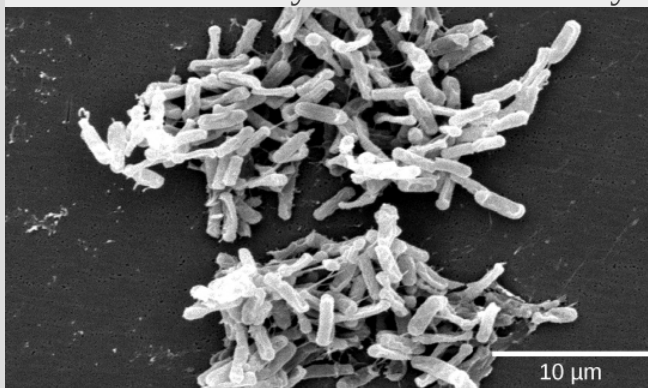
This scanning electron micrograph shows *Clostridium difficile*, a Gram-positive, rod-shaped bacterium that causes severe diarrhea. Infection commonly occurs after the normal gut fauna is eradicated by antibiotics. (credit: modification of work by CDC, HHS; scale-bar data from Matt Russell)

Scientists are also discovering that the absence of certain key microbes from our intestinal tract may set us up for a variety of problems. This seems to be particularly true regarding the appropriate functioning of the immune system. There are intriguing findings that suggest that the absence of these microbes is an important contributor to the development of allergies and some autoimmune disorders. Research is currently underway to test whether adding certain microbes to our internal ecosystem may help in the treatment of these problems as well as in treating some forms of autism.

Section Summary

Pathogens are only a small percentage of all prokaryotes. In fact, our life would not be possible without prokaryotes. Nitrogen is usually the most limiting element in terrestrial ecosystems; atmospheric nitrogen, the largest pool of available nitrogen, is unavailable to eukaryotes. Nitrogen can be "fixed," or converted into ammonia (NH_3) either biologically or abiotically. Biological nitrogen fixation (BNF) is exclusively carried out by prokaryotes. After photosynthesis, BNF is the second most important biological process on Earth. The most important source of BNF is the symbiotic interaction between soil bacteria and legume plants.

Microbial bioremediation is the use of microbial metabolism to remove pollutants. Bioremediation has been used to remove agricultural chemicals that leach from soil into groundwater and the subsurface. Toxic metals and oxides, such as selenium and arsenic compounds, can also be removed by bioremediation. Probably one of the most useful and interesting examples of the use of prokaryotes for bioremediation purposes is the cleanup of oil spills.

Human life is only possible due to the action of microbes, both those in the environment and those species that call us home. Internally, they help us digest our food, produce crucial nutrients for us, protect us from pathogenic microbes, and help train our immune systems to function correctly.

Review Questions

Exercise:

Problem: Which of these occurs through symbiotic nitrogen fixation?

a. The plant benefits from using an endless source of nitrogen.
b. The soil benefits from being naturally fertilized.
c. Bacteria benefit from using photosynthates from the plant.
d. All of the above occur.

Solution:

D

Exercise:

Problem:

Synthetic compounds found in an organism but not normally produced or expected to be present in that organism are called _____.

a. pesticides
b. bioremediators
c. recalcitrant compounds
d. xenobiotics

Solution:

D

Exercise:

Problem: Bioremediation includes _____.

a. the use of prokaryotes that can fix nitrogen
b. the use of prokaryotes to clean up pollutants

c. the use of prokaryotes as natural fertilizers
d. All of the above

Solution:

B

Free Response

Exercise:

Problem:

Your friend believes that prokaryotes are always detrimental and pathogenic. How would you explain to them that they are wrong?

Solution:

Remind them of the important roles prokaryotes play in decomposition and freeing up nutrients in biogeochemical cycles; remind them of the many prokaryotes that are not human pathogens and that fill very specialized niches. Furthermore, our normal bacterial symbionts are crucial for our digestion and in protecting us from pathogens.

Glossary

biological nitrogen fixation
   conversion of atmospheric nitrogen into ammonia exclusively carried out by prokaryotes

bioremediation
   use of microbial metabolism to remove pollutants

biotechnology
   any technological application that uses living organisms, biological systems, or their derivatives to produce or modify other products

nodule

> novel structure on the roots of certain plants (legumes) that results from the symbiotic interaction between the plant and soil bacteria, is the site of nitrogen fixation

Introduction

class="introduction"

The tobacco mosaic virus (left), seen here by transmission electron microscopy, was the first virus to be discovered. The virus causes disease in tobacco and other plants, such as the orchid (right). (credit a: USDA ARS; credit b: modification of work by USDA Forest Service, Department of Plant Pathology Archive North Carolina State

University;
scale-bar
data from
Matt
Russell)
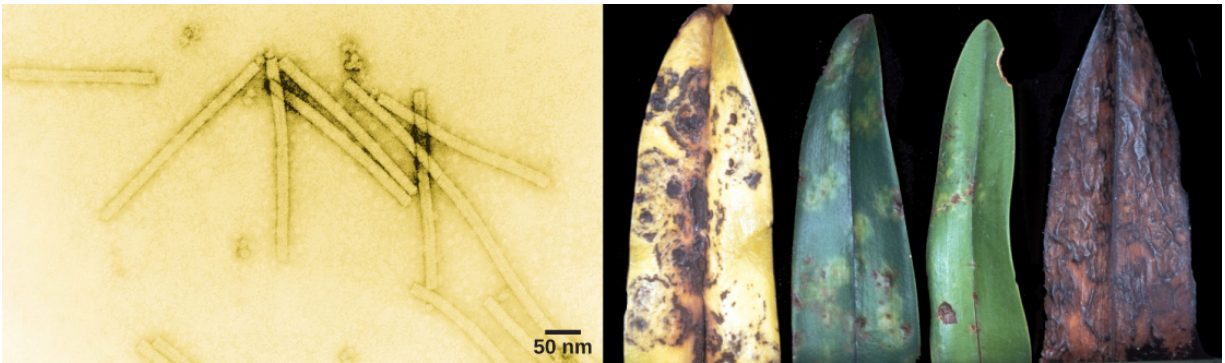
No one knows exactly when viruses emerged or from where they came, since viruses do not leave historical footprints such as fossils. Modern viruses are thought to be a mosaic of bits and pieces of nucleic acids picked up from various sources along their respective evolutionary paths. Viruses are acellular, parasitic entities that are not classified within any kingdom. Unlike most living organisms, viruses are not cells and cannot divide. Instead, they infect a host cell and use the host's replication processes to produce identical progeny virus particles. Viruses infect organisms as diverse as bacteria, plants, and animals. They exist in a netherworld between a living organism and a nonliving entity. Living things grow, metabolize, and reproduce. Viruses replicate, but to do so, they are entirely dependent on their host cells. They do not metabolize or grow, but are assembled in their mature form.

Viral Evolution, Morphology, and Classification
By the end of this section, you will be able to:

- Describe how viruses were first discovered and how they are detected
- Discuss three hypotheses about how viruses evolved
- Recognize the basic shapes of viruses
- Understand past and emerging classification systems for viruses

Viruses are diverse entities. They vary in their structure, their replication methods, and in their target hosts. Nearly all forms of life—from bacteria and archaea to eukaryotes such as plants, animals, and fungi—have viruses that infect them. While most biological diversity can be understood through evolutionary history, such as how species have adapted to conditions and environments, much about virus origins and evolution remains unknown.

Discovery and Detection

Viruses were first discovered after the development of a porcelain filter, called the Chamberland-Pasteur filter, which could remove all bacteria visible in the microscope from any liquid sample. In 1886, Adolph Meyer demonstrated that a disease of tobacco plants, tobacco mosaic disease, could be transferred from a diseased plant to a healthy one via liquid plant extracts. In 1892, Dmitri Ivanowski showed that this disease could be transmitted in this way even after the Chamberland-Pasteur filter had removed all viable bacteria from the extract. Still, it was many years before it was proven that these "filterable" infectious agents were not simply very small bacteria but were a new type of very small, disease-causing particle.

Virions, single virus particles, are very small, about 20–250 nanometers in diameter. These individual virus particles are the infectious form of a virus outside the host cell. Unlike bacteria (which are about 100-times larger), we cannot see viruses with a light microscope, with the exception of some large virions of the poxvirus family. It was not until the development of the electron microscope in the late 1930s that scientists got their first good view of the structure of the tobacco mosaic virus (TMV) ([link]) and other viruses ([link]). The surface structure of virions can be observed by both scanning and transmission electron microscopy, whereas the internal

structures of the virus can only be observed in images from a transmission electron microscope. The use of these technologies has allowed for the discovery of many viruses of all types of living organisms. They were initially grouped by shared morphology. Later, groups of viruses were classified by the type of nucleic acid they contained, DNA or RNA, and whether their nucleic acid was single- or double-stranded. More recently, molecular analysis of viral replicative cycles has further refined their classification.
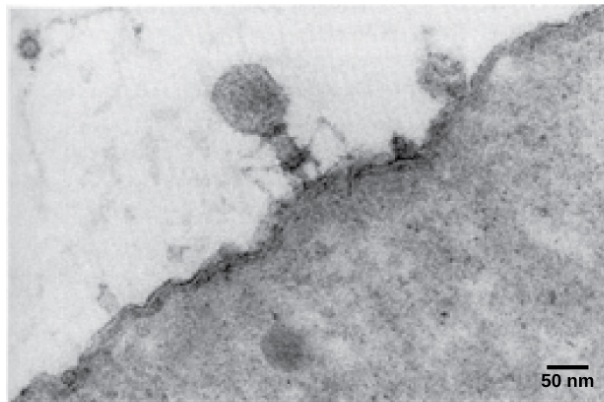
(a)
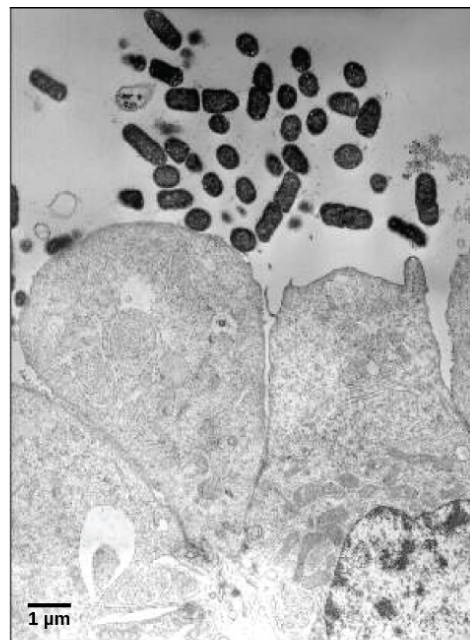
(b)

In these transmission electron micrographs, (a) a virus is dwarfed by the bacterial cell it infects, while (b) these *E. coli* cells are dwarfed by cultured colon cells. (credit a: modification of work by U.S. Dept. of Energy, Office of Science, LBL, PBD; credit b: modification of work by J.P. Nataro and S. Sears, unpub. data, CDC; scale-bar data from Matt Russell)

Evolution of Viruses

Although biologists have accumulated a significant amount of knowledge about how present-day viruses evolve, much less is known about how viruses originated in the first place. When exploring the evolutionary history of most organisms, scientists can look at fossil records and similar historic evidence. However, viruses do not fossilize, so researchers must conjecture by investigating how today's viruses evolve and by using biochemical and genetic information to create speculative virus histories.

While most findings agree that viruses don't have a single common ancestor, scholars have yet to find a single hypothesis about virus origins that is fully accepted in the field. One such hypothesis, called devolution or the regressive hypothesis, proposes to explain the origin of viruses by suggesting that viruses evolved from free-living cells. However, many components of how this process might have occurred are a mystery. A second hypothesis (called escapist or the progressive hypothesis) accounts for viruses having either an RNA or a DNA genome and suggests that viruses originated from RNA and DNA molecules that escaped from a host cell. A third hypothesis posits a system of self-replication similar to that of other self-replicating molecules, likely evolving alongside the cells they rely on as hosts; studies of some plant pathogens support this hypothesis.

As technology advances, scientists may develop and refine further hypotheses to explain the origin of viruses. The emerging field called virus molecular systematics attempts to do just that through comparisons of sequenced genetic material. These researchers hope to one day better understand the origin of viruses, a discovery that could lead to advances in the treatments for the ailments they produce.

Viral Morphology

Viruses are **acellular**, meaning they are biological entities that do not have a cellular structure. They therefore lack most of the components of cells, such as organelles, ribosomes, and the plasma membrane. A virion consists of a nucleic acid core, an outer protein coating or capsid, and sometimes an outer **envelope** made of protein and phospholipid membranes derived from

the host cell. Viruses may also contain additional proteins, such as enzymes. The most obvious difference between members of viral families is their morphology, which is quite diverse. An interesting feature of viral complexity is that the complexity of the host does not correlate with the complexity of the virion. Some of the most complex virion structures are observed in bacteriophages, viruses that infect the simplest living organisms, bacteria.

Morphology

Viruses come in many shapes and sizes, but these are consistent and distinct for each viral family. All virions have a nucleic acid genome covered by a protective layer of proteins, called a **capsid**. The capsid is made up of protein subunits called **capsomeres**. Some viral capsids are simple polyhedral "spheres," whereas others are quite complex in structure.

In general, the shapes of viruses are classified into four groups: filamentous, isometric (or icosahedral), enveloped, and head and tail. Filamentous viruses are long and cylindrical. Many plant viruses are filamentous, including TMV. Isometric viruses have shapes that are roughly spherical, such as poliovirus or herpesviruses. Enveloped viruses have membranes surrounding capsids. Animal viruses, such as HIV, are frequently enveloped. Head and tail viruses infect bacteria and have a head that is similar to icosahedral viruses and a tail shape like filamentous viruses.

Many viruses use some sort of glycoprotein to attach to their host cells via molecules on the cell called **viral receptors** ([link]). For these viruses, attachment is a requirement for later penetration of the cell membrane, so they can complete their replication inside the cell. The receptors that viruses use are molecules that are normally found on cell surfaces and have their own physiological functions. Viruses have simply evolved to make use of these molecules for their own replication. For example, HIV uses the CD4 molecule on T lymphocytes as one of its receptors. CD4 is a type of molecule called a cell adhesion molecule, which functions to keep different types of immune cells in close proximity to each other during the generation of a T lymphocyte immune response.
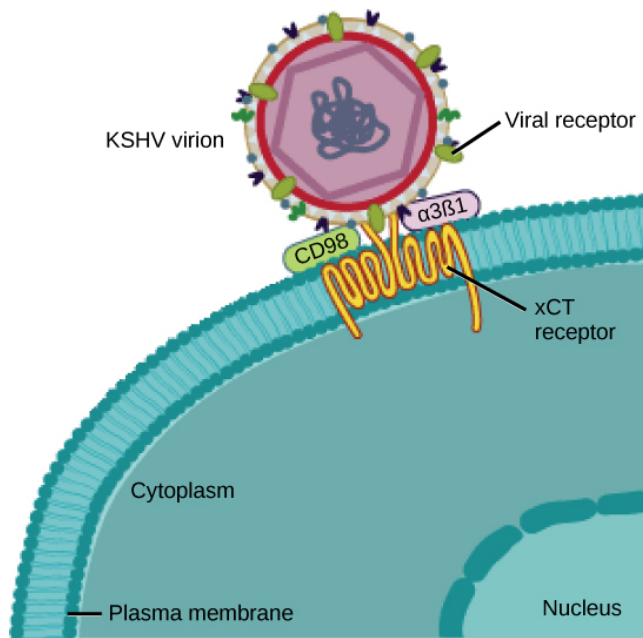
The KSHV virus binds the xCT receptor on the surface of human cells. xCT receptors protect cells against stress. Stressed cells express more xCT receptors than non-stressed cells. The KSHV virion causes cells to become stressed, thereby increasing expression of the receptor to which it binds. (credit: modification of work by NIAID, NIH)

Among the most complex virions known, the T4 bacteriophage, which infects the *Escherichia coli* bacterium, has a tail structure that the virus uses to attach to host cells and a head structure that houses its DNA.

Adenovirus, a non-enveloped animal virus that causes respiratory illnesses in humans, uses glycoprotein spikes protruding from its capsomeres to attach to host cells. Non-enveloped viruses also include those that cause

polio (poliovirus), plantar warts (papillomavirus), and hepatitis A (hepatitis A virus).

Enveloped virions like HIV, the causative agent in AIDS, consist of nucleic acid (RNA in the case of HIV) and capsid proteins surrounded by a phospholipid bilayer envelope and its associated proteins. Glycoproteins embedded in the viral envelope are used to attach to host cells. Other envelope proteins are the **matrix proteins** that stabilize the envelope and often play a role in the assembly of progeny virions. Chicken pox, influenza, and mumps are examples of diseases caused by viruses with envelopes. Because of the fragility of the envelope, non-enveloped viruses are more resistant to changes in temperature, pH, and some disinfectants than enveloped viruses.

Overall, the shape of the virion and the presence or absence of an envelope tell us little about what disease the virus may cause or what species it might infect, but they are still useful means to begin viral classification ([link]).

Note:
Art Connection
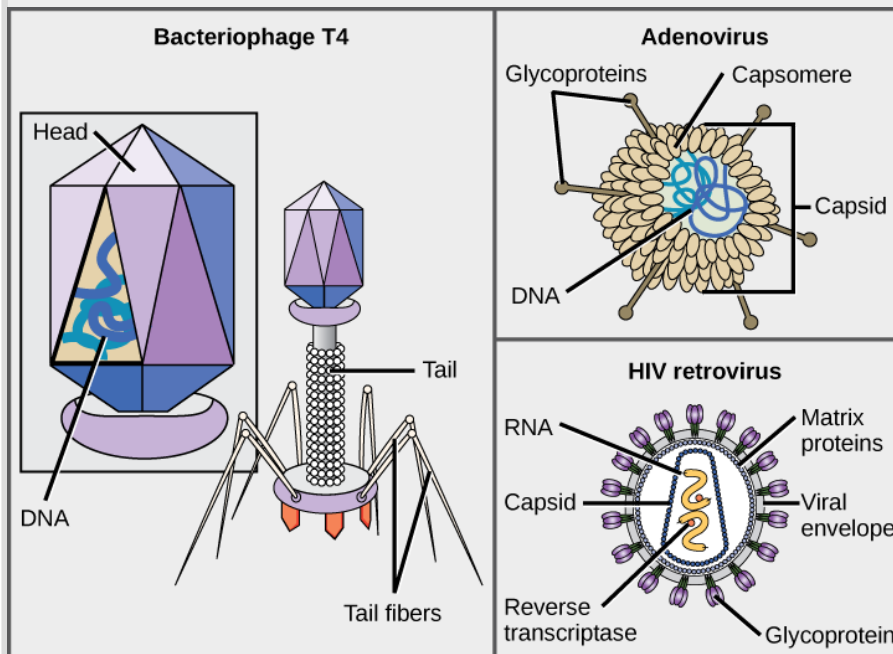
Viruses can be either complex in shape or relatively simple. This figure shows three relatively complex virions: the bacteriophage T4, with its DNA-containing head group and tail fibers that attach to host cells; adenovirus, which uses spikes from its capsid to bind to host cells; and HIV, which uses glycoproteins embedded in its envelope to bind to host cells. Notice that HIV has proteins called matrix proteins, internal to the envelope, which help stabilize virion shape. (credit "bacteriophage, adenovirus": modification of work by NCBI, NIH; credit "HIV retrovirus": modification of work by NIAID, NIH)

Which of the following statements about virus structure is true?

a. All viruses are encased in a viral membrane.
b. The capsomere is made up of small protein subunits called capsids.
c. DNA is the genetic material in all viruses.
d. Glycoproteins help the virus attach to the host cell.

Types of Nucleic Acid

Unlike nearly all living organisms that use DNA as their genetic material, viruses may use either DNA or RNA as theirs. The **virus core** contains the genome or total genetic content of the virus. Viral genomes tend to be small, containing only those genes that encode proteins that the virus cannot get from the host cell. This genetic material may be single- or double-stranded. It may also be linear or circular. While most viruses contain a single nucleic acid, others have genomes that have several, which are called segments.

In DNA viruses, the viral DNA directs the host cell's replication proteins to synthesize new copies of the viral genome and to transcribe and translate that genome into viral proteins. DNA viruses cause human diseases, such as

chickenpox, hepatitis B, and some venereal diseases, like herpes and genital warts.

RNA viruses contain only RNA as their genetic material. To replicate their genomes in the host cell, the RNA viruses encode enzymes that can replicate RNA into DNA, which cannot be done by the host cell. These RNA polymerase enzymes are more likely to make copying errors than DNA polymerases, and therefore often make mistakes during transcription. For this reason, mutations in RNA viruses occur more frequently than in DNA viruses. This causes them to change and adapt more rapidly to their host. Human diseases caused by RNA viruses include hepatitis C, measles, and rabies.

Virus Classification

To understand the features shared among different groups of viruses, a classification scheme is necessary. As most viruses are not thought to have evolved from a common ancestor, however, the methods that scientists use to classify living things are not very useful. Biologists have used several classification systems in the past, based on the morphology and genetics of the different viruses. However, these earlier classification methods grouped viruses differently, based on which features of the virus they were using to classify them. The most commonly used classification method today is called the Baltimore classification scheme and is based on how messenger RNA (mRNA) is generated in each particular type of virus.

Past Systems of Classification

Viruses are classified in several ways: by factors such as their core content ([link] and [link]), the structure of their capsids, and whether they have an outer envelope. The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures.

Virus Classification by Genome Structure and Core	
Core Classifications	**Examples**
- RNA - DNA	- Rabies virus, retroviruses - Herpesviruses, smallpox virus
- Single-stranded - Double-stranded	- Rabies virus, retroviruses - Herpesviruses, smallpox virus
- Linear - Circular	Rabies virus, retroviruses, herpesviruses, smallpox virus Papillomaviruses, many bacteriophages
- Non-segmented: genome consists of a single segment of genetic material - Segmented: genome is divided into multiple segments	Parainfluenza viruses Influenza viruses

Viral envelope   Matrix proteins   Glycoprotein

Matrix proteins and viral envelope

Capsid

dsDNA

Capsid   ssRNA

50 nm

50 nm
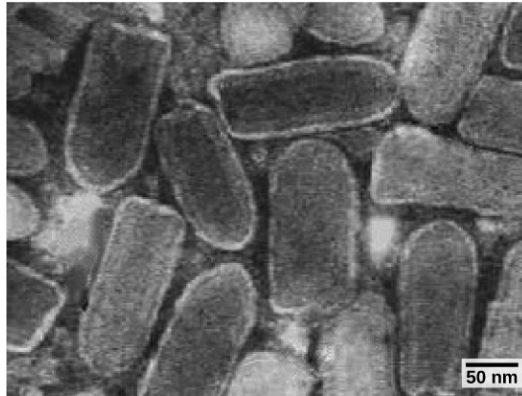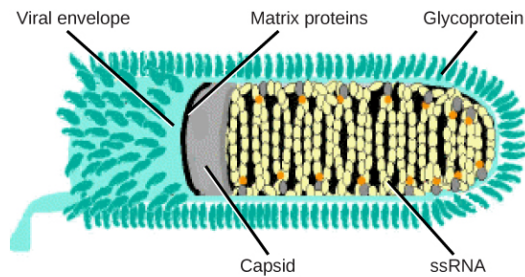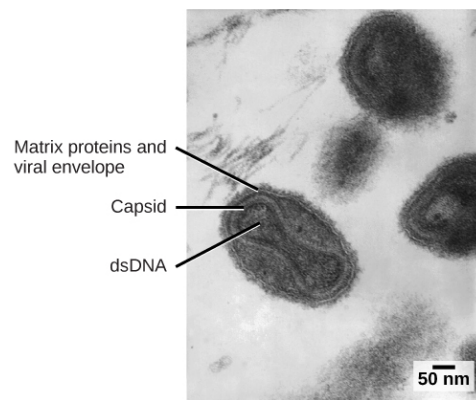
(a) Rabies virus

(b) Variola virus

Viruses are classified based on their core genetic material and capsid design. (a) Rabies virus has a single-stranded RNA (ssRNA) core and an enveloped helical capsid, whereas (b) variola virus, the causative agent of smallpox, has a double-stranded DNA (dsDNA) core and a complex capsid. Rabies transmission occurs when saliva from an infected mammal enters a wound. The virus travels through neurons in the peripheral nervous system to the central nervous system where it impairs brain function, and then travels to other tissues. The virus can infect any mammal, and most die within weeks of infection. Smallpox is a human virus transmitted by inhalation of the variola virus, localized in the skin, mouth, and throat, which causes a characteristic rash. Before its eradication in 1979, infection resulted in a 30–35 percent mortality rate. (credit "rabies diagram": modification of work by CDC; "rabies micrograph": modification of work by Dr. Fred Murphy, CDC; credit "small pox micrograph": modification of work by Dr. Fred Murphy, Sylvia Whitfield, CDC; credit "smallpox photo": modification of work by CDC; scale-bar data from Matt Russell)

Viruses can also be classified by the design of their capsids ([link] and [link]). Capsids are classified as naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex ([link] and [link]). The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures ([link]).
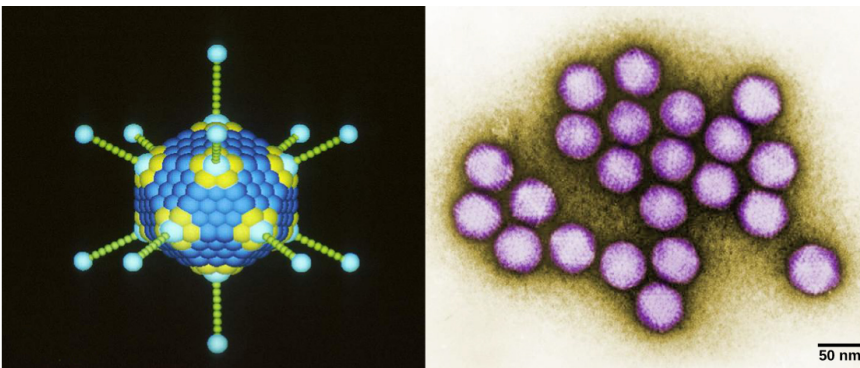
Adenovirus (left) is depicted with a double-stranded DNA genome enclosed in an icosahedral capsid that is 90–100 nm across. The virus, shown clustered in the micrograph (right), is transmitted orally and causes a variety of illnesses in vertebrates, including human eye and respiratory infections. (credit "adenovirus": modification of work by Dr. Richard Feldmann, National Cancer Institute; credit "micrograph": modification of work by Dr. G. William Gary, Jr., CDC; scale-bar data from Matt Russell)

Virus Classification by Capsid Structure	
Capsid Classification	**Examples**
Naked icosahedral	Hepatitis A virus, polioviruses
Enveloped icosahedral	Epstein-Barr virus, herpes simplex virus, rubella virus, yellow fever virus, HIV-1
Enveloped helical	Influenza viruses, mumps virus, measles virus, rabies virus
Naked helical	Tobacco mosaic virus
Complex with many proteins; some have combinations of icosahedral and helical capsid structures	Herpesviruses, smallpox virus, hepatitis B virus, T4 bacteriophage
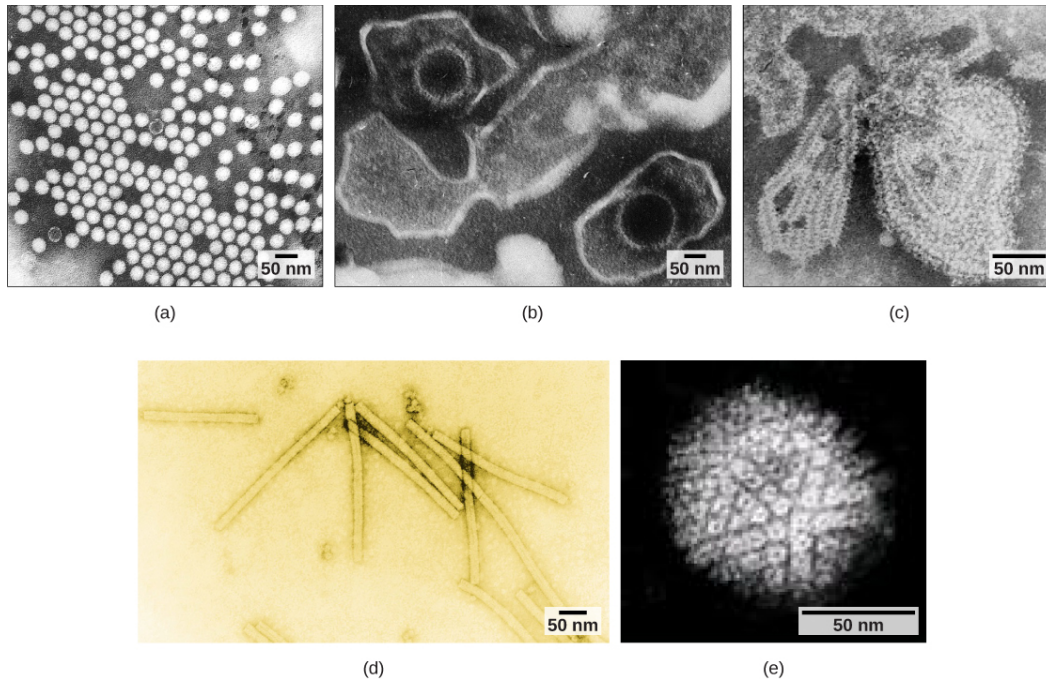
Transmission electron micrographs of various viruses show their structures. The capsid of the (a) polio virus is naked icosahedral; (b) the Epstein-Barr virus capsid is enveloped icosahedral; (c) the mumps virus capsid is an enveloped helix; (d) the tobacco mosaic virus capsid is naked helical; and (e) the herpesvirus capsid is complex. (credit a: modification of work by Dr. Fred Murphy, Sylvia Whitfield; credit b: modification of work by Liza Gross; credit c: modification of work by Dr. F. A. Murphy, CDC; credit d: modification of work by USDA ARS; credit e: modification of work by Linda Stannard, Department of Medical Microbiology, University of Cape Town, South Africa, NASA; scale-bar data from Matt Russell)

Baltimore Classification

The most commonly used system of virus classification was developed by Nobel Prize-winning biologist David Baltimore in the early 1970s. In

addition to the differences in morphology and genetics mentioned above, the Baltimore classification scheme groups viruses according to how the mRNA is produced during the replicative cycle of the virus.

Group I viruses contain double-stranded DNA (dsDNA) as their genome. Their mRNA is produced by transcription in much the same way as with cellular DNA. **Group II** viruses have single-stranded DNA (ssDNA) as their genome. They convert their single-stranded genomes into a dsDNA intermediate before transcription to mRNA can occur. **Group III** viruses use dsRNA as their genome. The strands separate, and one of them is used as a template for the generation of mRNA using the RNA-dependent RNA polymerase encoded by the virus. **Group IV** viruses have ssRNA as their genome with a positive polarity. **Positive polarity** means that the genomic RNA can serve directly as mRNA. Intermediates of dsRNA, called **replicative intermediates**, are made in the process of copying the genomic RNA. Multiple, full-length RNA strands of negative polarity (complimentary to the positive-stranded genomic RNA) are formed from these intermediates, which may then serve as templates for the production of RNA with positive polarity, including both full-length genomic RNA and shorter viral mRNAs. **Group V** viruses contain ssRNA genomes with a **negative polarity**, meaning that their sequence is complementary to the mRNA. As with Group IV viruses, dsRNA intermediates are used to make copies of the genome and produce mRNA. In this case, the negative-stranded genome can be converted directly to mRNA. Additionally, full-length positive RNA strands are made to serve as templates for the production of the negative-stranded genome. **Group VI** viruses have diploid (two copies) ssRNA genomes that must be converted, using the enzyme **reverse transcriptase**, to dsDNA; the dsDNA is then transported to the nucleus of the host cell and inserted into the host genome. Then, mRNA can be produced by transcription of the viral DNA that was integrated into the host genome. **Group VII** viruses have partial dsDNA genomes and make ssRNA intermediates that act as mRNA, but are also converted back into dsDNA genomes by reverse transcriptase, necessary for genome replication. The characteristics of each group in the Baltimore classification are summarized in [link] with examples of each group.

Baltimore Classification

Group	Characteristics	Mode of mRNA Production	Example
I	Double-stranded DNA	mRNA is transcribed directly from the DNA template	Herpes simplex (herpesvirus)
II	Single-stranded DNA	DNA is converted to double-stranded form before RNA is transcribed	Canine parvovirus (parvovirus)
III	Double-stranded RNA	mRNA is transcribed from the RNA genome	Childhood gastroenteritis (rotavirus)
IV	Single stranded RNA (+)	Genome functions as mRNA	Common cold (pircornavirus)
V	Single stranded RNA (-)	mRNA is transcribed from the RNA genome	Rabies (rhabdovirus)

Baltimore Classification			
Group	**Characteristics**	**Mode of mRNA Production**	**Example**
VI	Single stranded RNA viruses with reverse transcriptase	Reverse transcriptase makes DNA from the RNA genome; DNA is then incorporated in the host genome; mRNA is transcribed from the incorporated DNA	Human immunodeficiency virus (HIV)

Baltimore Classification			
Group	**Characteristics**	**Mode of mRNA Production**	**Example**
VII	Double stranded DNA viruses with reverse transcriptase	The viral genome is double-stranded DNA, but viral DNA is replicated through an RNA intermediate; the RNA may serve directly as mRNA or as a template to make mRNA	Hepatitis B virus (hepadnavirus)

Section Summary

Viruses are tiny, acellular entities that can usually only be seen with an electron microscope. Their genomes contain either DNA or RNA—never both—and they replicate using the replication proteins of a host cell. Viruses are diverse, infecting archaea, bacteria, fungi, plants, and animals. Viruses consist of a nucleic acid core surrounded by a protein capsid with or without an outer lipid envelope. The capsid shape, presence of an envelope, and core composition dictate some elements of the classification of viruses. The most commonly used classification method, the Baltimore classification, categorizes viruses based on how they produce their mRNA.

Art Connections

Exercise:

Problem:

[link] Which of the following statements about virus structure is true?

   a. All viruses are encased in a viral membrane.
   b. The capsomere is made up of small protein subunits called capsids.
   c. DNA is the genetic material in all viruses.
   d. Glycoproteins help the virus attach to the host cell.

Solution:

[link] D

Review Questions

Exercise:

Problem: Which statement is true?

   a. A virion contains DNA and RNA.
   b. Viruses are acellular.
   c. Viruses replicate outside of the cell.
   d. Most viruses are easily visualized with a light microscope.

Solution:

B

Exercise:

Problem:

The viral _____ plays a role in attaching a virion to the host cell.

    a. core
    b. capsid
    c. envelope
    d. both b and c

Solution:

D

Exercise:

Problem: Viruses_____.

    a. all have a round shape
    b. cannot have a long shape
    c. do not maintain any shape
    d. vary in shape

Solution:

D

Free Response

Exercise:

Problem:

The first electron micrograph of a virus (tobacco mosaic virus) was produced in 1939. Before that time, how did scientists know that viruses existed if they could not see them? (Hint: Early scientists called viruses "filterable agents.")

Solution:

Viruses pass through filters that eliminated all bacteria that were visible in the light microscopes at the time. As the bacteria-free filtrate could still cause infections when given to a healthy organism, this observation demonstrated the existence of very small infectious agents. These agents were later shown to be unrelated to bacteria and were classified as viruses.

Glossary

acellular
>   lacking cells

capsid
>   protein coating of the viral core

capsomere
>   protein subunit that makes up the capsid

envelope
>   lipid bilayer that envelopes some viruses

group I virus
>   virus with a dsDNA genome

group II virus
>   virus with a ssDNA genome

group III virus
>   virus with a dsRNA genome

group IV virus
>   virus with a ssRNA genome with positive polarity

group V virus
>   virus with a ssRNA genome with negative polarity

group VI virus
  virus with a ssRNA genomes converted into dsDNA by reverse transcriptase

group VII virus
  virus with a single-stranded mRNA converted into dsDNA for genome replication

matrix protein
  envelope protein that stabilizes the envelope and often plays a role in the assembly of progeny virions

negative polarity
  ssRNA viruses with genomes complimentary to their mRNA

positive polarity
  ssRNA virus with a genome that contains the same base sequences and codons found in their mRNA

replicative intermediate
  dsRNA intermediate made in the process of copying genomic RNA

reverse transcriptase
  enzyme found in Baltimore groups VI and VII that converts single-stranded RNA into double-stranded DNA

viral receptor
  glycoprotein used to attach a virus to host cells via molecules on the cell

virion
  individual virus particle outside a host cell

virus core
  contains the virus genome

Virus Infections and Hosts
By the end of this section, you will be able to:

- List the steps of replication and explain what occurs at each step
- Describe the lytic and lysogenic cycles of virus replication
- Explain the transmission and diseases of animal and plant viruses
- Discuss the economic impact of animal and plant viruses

Viruses can be seen as obligate, intracellular parasites. A virus must attach to a living cell, be taken inside, manufacture its proteins and copy its genome, and find a way to escape the cell so that the virus can infect other cells. Viruses can infect only certain species of hosts and only certain cells within that host. Cells that a virus may use to replicate are called **permissive**. For most viruses, the molecular basis for this specificity is that a particular surface molecule known as the viral receptor must be found on the host cell surface for the virus to attach. Also, metabolic and host cell immune response differences seen in different cell types based on differential gene expression are a likely factor in which cells a virus may target for replication. The permissive cell must make the substances that the virus needs or the virus will not be able to replicate there.

Steps of Virus Infections

A virus must use cell processes to replicate. The viral replication cycle can produce dramatic biochemical and structural changes in the host cell, which may cause cell damage. These changes, called **cytopathic** (causing cell damage) effects, can change cell functions or even destroy the cell. Some infected cells, such as those infected by the common cold virus known as rhinovirus, die through **lysis** (bursting) or apoptosis (programmed cell death or "cell suicide"), releasing all progeny virions at once. The symptoms of viral diseases result from the immune response to the virus, which attempts to control and eliminate the virus from the body, and from cell damage caused by the virus. Many animal viruses, such as HIV (human immunodeficiency virus), leave the infected cells of the immune system by a process known as **budding**, where virions leave the cell individually. During the budding process, the cell does not undergo lysis and is not immediately killed. However, the damage to the cells that the virus infects

may make it impossible for the cells to function normally, even though the cells remain alive for a period of time. Most productive viral infections follow similar steps in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release ([link]).

Attachment

A virus attaches to a specific receptor site on the host cell membrane through attachment proteins in the capsid or via glycoproteins embedded in the viral envelope. The specificity of this interaction determines the host—and the cells within the host—that can be infected by a particular virus. This can be illustrated by thinking of several keys and several locks, where each key will fit only one specific lock.

Note:
Link to Learning

This video explains how influenza attacks the body.

Entry

The nucleic acid of bacteriophages enters the host cell naked, leaving the capsid outside the cell. Plant and animal viruses can enter through endocytosis, in which the cell membrane surrounds and engulfs the entire virus. Some enveloped viruses enter the cell when the viral envelope fuses directly with the cell membrane. Once inside the cell, the viral capsid is

degraded, and the viral nucleic acid is released, which then becomes available for replication and transcription.

Replication and Assembly

The replication mechanism depends on the viral genome. DNA viruses usually use host cell proteins and enzymes to make additional DNA that is transcribed to messenger RNA (mRNA), which is then used to direct protein synthesis. RNA viruses usually use the RNA core as a template for synthesis of viral genomic RNA and mRNA. The viral mRNA directs the host cell to synthesize viral enzymes and capsid proteins, and assemble new virions. Of course, there are exceptions to this pattern. If a host cell does not provide the enzymes necessary for viral replication, viral genes supply the information to direct synthesis of the missing proteins. Retroviruses, such as HIV, have an RNA genome that must be reverse transcribed into DNA, which then is incorporated into the host cell genome. They are within group VI of the Baltimore classification scheme. To convert RNA into DNA, retroviruses must contain genes that encode the virus-specific enzyme reverse transcriptase that transcribes an RNA template to DNA. Reverse transcription never occurs in uninfected host cells—the needed enzyme reverse transcriptase is only derived from the expression of viral genes within the infected host cells. The fact that HIV produces some of its own enzymes not found in the host has allowed researchers to develop drugs that inhibit these enzymes. These drugs, including the reverse transcriptase inhibitor **AZT**, inhibit HIV replication by reducing the activity of the enzyme without affecting the host's metabolism. This approach has led to the development of a variety of drugs used to treat HIV and has been effective at reducing the number of infectious virions (copies of viral RNA) in the blood to non-detectable levels in many HIV-infected individuals.

Egress

The last stage of viral replication is the release of the new virions produced in the host organism, where they are able to infect adjacent cells and repeat

the replication cycle. As you've learned, some viruses are released when the host cell dies, and other viruses can leave infected cells by budding through the membrane without directly killing the cell.

Art Connection

1. Influenza virus becomes attached to a target epithelial cell.

2. The cell engulfs the virus by endocytosis.

3. Viral contents are released. Viral RNA enters the nucleus where it is replicated by the viral RNA polymerase.

4. Viral mRNA is used to make viral proteins.

5. New viral particles are made and released into the extracellular fluid. The cell, which is not killed in the process, continues to make new virus.

In influenza virus infection, glycoproteins attach to a host epithelial cell. As a result, the virus is engulfed. RNA and proteins are made and assembled into new virions.

Influenza virus is packaged in a viral envelope that fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

Different Hosts and Their Viruses

As you've learned, viruses are often very specific as to which hosts and which cells within the host they will infect. This feature of a virus makes it specific to one or a few species of life on Earth. On the other hand, so many different types of viruses exist on Earth that nearly every living organism has its own set of viruses that tries to infect its cells. Even the smallest and simplest of cells, prokaryotic bacteria, may be attacked by specific types of viruses.

Bacteriophages
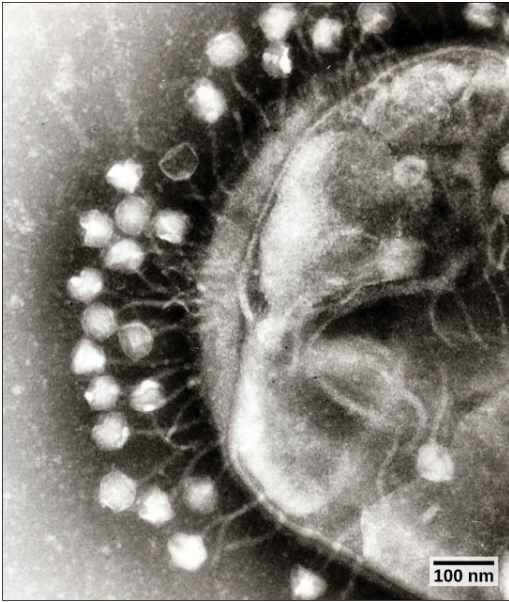
This transmission electron micrograph shows bacteriophages attached to a bacterial cell. (credit: modification of work by Dr. Graham Beards; scale-bar data from Matt Russell)

Bacteriophages are viruses that infect bacteria ([link]). When infection of a cell by a bacteriophage results in the production of new virions, the infection is said to be **productive**. If the virions are released by bursting the cell, the virus replicates by means of a **lytic cycle** ([link]). An example of a lytic bacteriophage is T4, which infects *Escherichia coli* found in the human intestinal tract. Sometimes, however, a virus can remain within the cell without being released. For example, when a temperate bacteriophage infects a bacterial cell, it replicates by means of a **lysogenic cycle** ([link]), and the viral genome is incorporated into the genome of the host cell. When the phage DNA is incorporated into the host cell genome, it is called a **prophage**. An example of a lysogenic bacteriophage is the λ (lambda) virus, which also infects the *E. coli* bacterium. Viruses that infect plant or

animal cells may also undergo infections where they are not producing virions for long periods. An example is the animal herpesviruses, including herpes simplex viruses, the cause of oral and genital herpes in humans. In a process called **latency**, these viruses can exist in nervous tissue for long periods of time without producing new virions, only to leave latency periodically and cause lesions in the skin where the virus replicates. Even though there are similarities between lysogeny and latency, the term lysogenic cycle is usually reserved to describe bacteriophages. Latency will be described in more detail below.

Note:

Art Connection

Lytic cycle

The phage infects a cell.

The phage DNA circularizes, remaining separate from the host DNA.

Phage DNA replicates and phage proteins are made. New phage particles are assembled.

The cell lyses, releasing phage.

Lysogenic cycle

The phage infects a cell.

The phage DNA becomes incorporated into the host genome.

The cell divides, and prophage DNA is passed on to daughter cells.

Under stressful conditions, the phage DNA is excised from the bacterial chromosome and enters the lytic cycle.

A temperate bacteriophage has both lytic and lysogenic cycles. In the lytic cycle, the phage replicates and lyses the host cell. In the lysogenic cycle, phage DNA is incorporated into the host genome, where it is passed on to subsequent generations. Environmental stressors such as starvation or

exposure to toxic chemicals may cause the prophage to
excise and enter the lytic cycle.

Which of the following statements is false?

a. In the lytic cycle, new phage are produced and released into the environment.
b. In the lysogenic cycle, phage DNA is incorporated into the host genome.
c. An environmental stressor can cause the phage to initiate the lysogenic cycle.
d. Cell lysis only occurs in the lytic cycle.

Animal Viruses

Animal viruses, unlike the viruses of plants and bacteria, do not have to penetrate a cell wall to gain access to the host cell. Non-enveloped or "naked" animal viruses may enter cells in two different ways. As a protein in the viral capsid binds to its receptor on the host cell, the virus may be taken inside the cell via a vesicle during the normal cell process of receptor-mediated endocytosis. An alternative method of cell penetration used by non-enveloped viruses is for capsid proteins to undergo shape changes after binding to the receptor, creating channels in the host cell membrane. The viral genome is then "injected" into the host cell through these channels in a manner analogous to that used by many bacteriophages. Enveloped viruses also have two ways of entering cells after binding to their receptors: receptor-mediated endocytosis, or **fusion**. Many enveloped viruses enter the cell by receptor-mediated endocytosis in a fashion similar to some non-enveloped viruses. On the other hand, fusion only occurs with enveloped virions. These viruses, which include HIV among others, use special fusion proteins in their envelopes to cause the envelope to fuse with the plasma membrane of the cell, thus releasing the genome and capsid of the virus into the cell cytoplasm.

After making their proteins and copying their genomes, animal viruses complete the assembly of new virions and exit the cell. As we have already discussed using the example of HIV, enveloped animal viruses may bud from the cell membrane as they assemble themselves, taking a piece of the cell's plasma membrane in the process. On the other hand, non-enveloped viral progeny, such as rhinoviruses, accumulate in infected cells until there is a signal for lysis or apoptosis, and all virions are released together.

As you will learn in the next module, animal viruses are associated with a variety of human diseases. Some of them follow the classic pattern of **acute disease**, where symptoms get increasingly worse for a short period followed by the elimination of the virus from the body by the immune system and eventual recovery from the infection. Examples of acute viral diseases are the common cold and influenza. Other viruses cause long-term **chronic infections**, such as the virus causing hepatitis C, whereas others, like herpes simplex virus, only cause **intermittent** symptoms. Still other viruses, such as human herpesviruses 6 and 7, which in some cases can cause the minor childhood disease roseola, often successfully cause productive infections without causing any symptoms at all in the host, and thus we say these patients have an **asymptomatic infection**.

In hepatitis C infections, the virus grows and reproduces in liver cells, causing low levels of liver damage. The damage is so low that infected individuals are often unaware that they are infected, and many infections are detected only by routine blood work on patients with risk factors such as intravenous drug use. On the other hand, since many of the symptoms of viral diseases are caused by immune responses, a lack of symptoms is an indication of a weak immune response to the virus. This allows for the virus to escape elimination by the immune system and persist in individuals for years, all the while producing low levels of progeny virions in what is known as a chronic viral disease. Chronic infection of the liver by this virus leads to a much greater chance of developing liver cancer, sometimes as much as 30 years after the initial infection.

As already discussed, herpes simplex virus can remain in a state of latency in nervous tissue for months, even years. As the virus "hides" in the tissue and makes few if any viral proteins, there is nothing for the immune

response to act against, and immunity to the virus slowly declines. Under certain conditions, including various types of physical and psychological stress, the latent herpes simplex virus may be reactivated and undergo a lytic replication cycle in the skin, causing the lesions associated with the disease. Once virions are produced in the skin and viral proteins are synthesized, the immune response is again stimulated and resolves the skin lesions in a few days by destroying viruses in the skin. As a result of this type of replicative cycle, appearances of cold sores and genital herpes outbreaks only occur intermittently, even though the viruses remain in the nervous tissue for life. Latent infections are common with other herpesviruses as well, including the varicella-zoster virus that causes chickenpox. After having a chickenpox infection in childhood, the varicella-zoster virus can remain latent for many years and reactivate in adults to cause the painful condition known as "shingles" ([link]**ab**).

<div align="center">(a)   (b)</div>
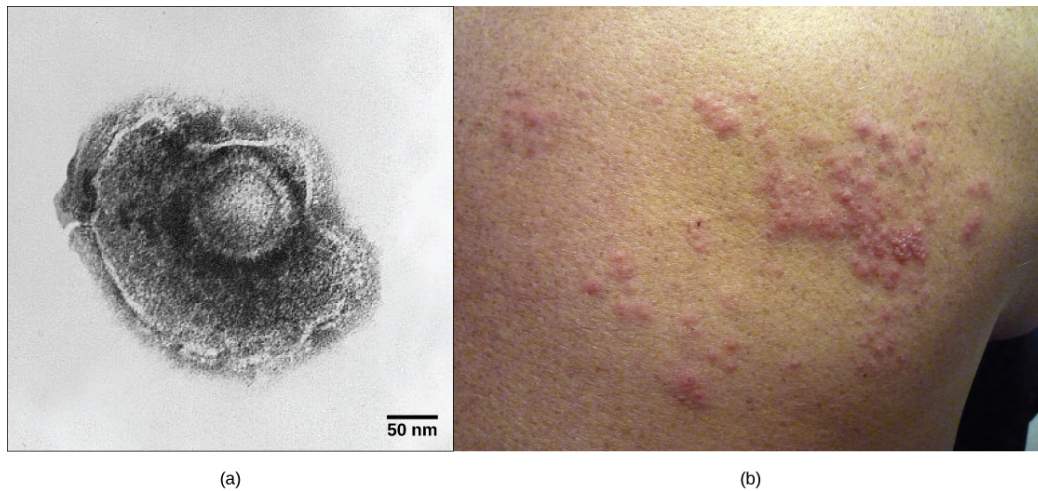
(a) Varicella-zoster, the virus that causes chickenpox, has an enveloped icosahedral capsid visible in this transmission electron micrograph. Its double-stranded DNA genome becomes incorporated in the host DNA and can reactivate after latency in the form of (b) shingles, often exhibiting a rash. (credit a: modification of work by Dr. Erskine Palmer, B. G. Martin, CDC; credit b: modification of work by "rosmary"/Flickr; scale-bar data from Matt Russell)

Some animal-infecting viruses, including the hepatitis C virus discussed above, are known as **oncogenic viruses**: They have the ability to cause cancer. These viruses interfere with the normal regulation of the host cell cycle either by either introducing genes that stimulate unregulated cell growth (oncogenes) or by interfering with the expression of genes that inhibit cell growth. Oncogenic viruses can be either DNA or RNA viruses. Cancers known to be associated with viral infections include cervical cancer caused by human papillomavirus (HPV) ([link]), liver cancer caused by hepatitis B virus, T-cell leukemia, and several types of lymphoma.
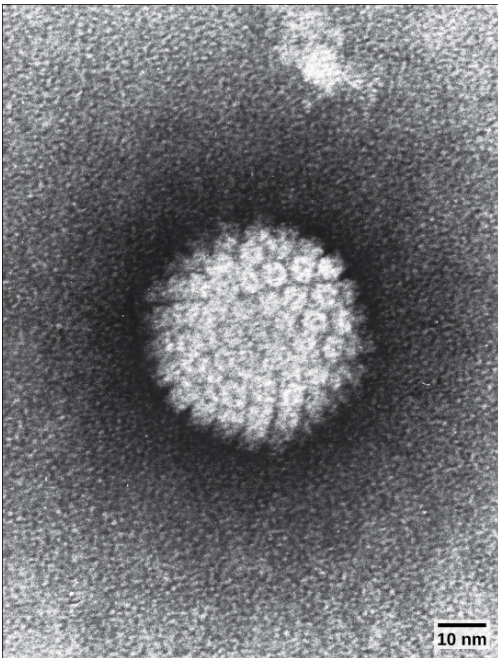
HPV, or human papillomavirus, has a naked icosahedral capsid visible in this transmission electron micrograph and a double-stranded DNA genome that is incorporated into

the host DNA. The virus, which is sexually transmitted, is oncogenic and can lead to cervical cancer. (credit: modification of work by NCI, NIH; scale-bar data from Matt Russell)

Plant Viruses

Plant viruses, like other viruses, contain a core of either DNA or RNA. You have already learned about one of these, the tobacco mosaic virus. As plant cells have a cell wall to protect their cells, these viruses do not use receptor-mediated endocytosis to enter host cells as is seen with animal viruses. For many plant viruses to be transferred from plant to plant, damage to some of the plants' cells must occur to allow the virus to enter a new host. This damage is often caused by weather, insects, animals, fire, or human activities like farming or landscaping. Additionally, plant offspring may

inherit viral diseases from parent plants. Plant viruses can be transmitted by a variety of vectors, through contact with an infected plant's sap, by living organisms such as insects and nematodes, and through pollen. When plants viruses are transferred between different plants, this is known as **horizontal transmission**, and when they are inherited from a parent, this is called **vertical transmission**.

Symptoms of viral diseases vary according to the virus and its host ([link]). One common symptom is **hyperplasia**, the abnormal proliferation of cells that causes the appearance of plant tumors known as **galls**. Other viruses induce **hypoplasia**, or decreased cell growth, in the leaves of plants, causing thin, yellow areas to appear. Still other viruses affect the plant by directly killing plant cells, a process known as **cell necrosis**. Other symptoms of plant viruses include malformed leaves, black streaks on the stems of the plants, altered growth of stems, leaves, or fruits, and ring spots, which are circular or linear areas of discoloration found in a leaf.

Some Common Symptoms of Plant Viral Diseases	
Symptom	**Appears as**
Hyperplasia	Galls (tumors)
Hypoplasia	Thinned, yellow splotches on leaves
Cell necrosis	Dead, blackened stems, leaves, or fruit
Abnormal growth patterns	Malformed stems, leaves, or fruit
Discoloration	Yellow, red, or black lines, or rings in stems, leaves, or fruit

Plant viruses can seriously disrupt crop growth and development, significantly affecting our food supply. They are responsible for poor crop quality and quantity globally, and can bring about huge economic losses annually. Others viruses may damage plants used in landscaping. Some viruses that infect agricultural food plants include the name of the plant they infect, such as tomato spotted wilt virus, bean common mosaic virus, and cucumber mosaic virus. In plants used for landscaping, two of the most common viruses are peony ring spot and rose mosaic virus. There are far too many plant viruses to discuss each in detail, but symptoms of bean common mosaic virus result in lowered bean production and stunted, unproductive plants. In the ornamental rose, the rose mosaic disease causes wavy yellow lines and colored splotches on the leaves of the plant.

Section Summary

Viral replication within a living cell always produces changes in the cell, sometimes resulting in cell death and sometimes slowly killing the infected cells. There are six basic stages in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release. A viral infection may be productive, resulting in new virions, or nonproductive, which means that the virus remains inside the cell without producing new virions. Bacteriophages are viruses that infect bacteria. They have two different modes of replication: the lytic cycle, where the virus replicates and bursts out of the bacteria, and the lysogenic cycle, which involves the incorporation of the viral genome into the bacterial host genome. Animal viruses cause a variety of infections, with some causing chronic symptoms (hepatitis C), some intermittent symptoms (latent viruses such a herpes simplex virus 1), and others that cause very few symptoms, if any (human herpesviruses 6 and 7). Oncogenic viruses in animals have the ability to cause cancer by interfering with the regulation of the host cell cycle. Viruses of plants are responsible for significant economic damage in both agriculture and plants used for ornamentation.

Art Connections

Exercise:

Problem:

[link] Influenza virus is packaged in a viral envelope that fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

Solution:

[link] The host cell can continue to make new virus particles.

Exercise:

Problem: [link] Which of the following statements is false?

    a. In the lytic cycle, new phage are produced and released into the environment.
    b. In the lysogenic cycle, phage DNA is incorporated into the host genome.
    c. An environmental stressor can cause the phage to initiate the lysogenic cycle.
    d. Cell lysis only occurs in the lytic cycle.

Solution:

[link] C

Review Questions

Exercise:

Problem: Which statement is *not* true of viral replication?

    a. A lysogenic cycle kills the host cell.
    b. There are six basic steps in the viral replication cycle.
    c. Viral replication does not affect host cell function.

d. Newly released virions can infect adjacent cells.

Solution:

D

Exercise:

Problem: Which statement is true of viral replication?

 a. In the process of apoptosis, the cell survives.
 b. During attachment, the virus attaches at specific sites on the cell surface.
 c. The viral capsid helps the host cell produce more copies of the viral genome.
 d. mRNA works outside of the host cell to produce enzymes and proteins.

Solution:

B

Exercise:

Problem: Which statement is true of reverse transcriptase?

 a. It is a nucleic acid.
 b. It infects cells.
 c. It transcribes RNA to make DNA.
 d. It is a lipid.

Solution:

C

Exercise:

Problem: Oncogenic virus cores can be_____.

    a. RNA
    b. DNA
    c. neither RNA nor DNA
    d. either RNA or DNA

Solution:

D

Exercise:

Problem: Which is true of DNA viruses?

    a. They use the host cell's machinery to produce new copies of their genome.
    b. They all have envelopes.
    c. They are the only kind of viruses that can cause cancer.
    d. They are not important plant pathogens.

Solution:

A

Exercise:

Problem:A bacteriophage can infect _____.

    a. the lungs
    b. viruses
    c. prions
    d. bacteria

Solution:

D

Free Response

Exercise:

Problem: Why can't dogs catch the measles?

Solution:

The virus can't attach to dog cells, because dog cells do not express the receptors for the virus and/or there is no cell within the dog that is permissive for viral replication.

Exercise:

Problem:

One of the first and most important targets for drugs to fight infection with HIV (a retrovirus) is the reverse transcriptase enzyme. Why?

Solution:

Reverse transcriptase is needed to make more HIV-1 viruses, so targeting the reverse transcriptase enzyme may be a way to inhibit the replication of the virus. Importantly, by targeting reverse transcriptase, we do little harm to the host cell, since host cells do not make reverse transcriptase. Thus, we can specifically attack the virus and not the host cell when we use reverse transcriptase inhibitors.

Exercise:

Problem:

In this section, you were introduced to different types of viruses and viral diseases. Briefly discuss the most interesting or surprising thing you learned about viruses.

Solution:

Answer is open and will vary.

Exercise:

Problem:

Although plant viruses cannot infect humans, what are some of the ways in which they affect humans?

Solution:

Plant viruses infect crops, causing crop damage and failure, and considerable economic losses.

Glossary

acute disease
    disease where the symptoms rise and fall within a short period of time

asymptomatic disease
    disease where there are no symptoms and the individual is unaware of being infected unless lab tests are performed

AZT
    anti-HIV drug that inhibits the viral enzyme reverse transcriptase

bacteriophage
    virus that infects bacteria

budding

method of exit from the cell used in certain animal viruses, where virions leave the cell individually by capturing a piece of the host plasma membrane

cell necrosis
    cell death

chronic infection
    describes when the virus persists in the body for a long period of time

cytopathic
    causing cell damage

fusion
    method of entry by some enveloped viruses, where the viral envelope fuses with the plasma membrane of the host cell

gall
    appearance of a plant tumor

horizontal transmission
    transmission of a disease between unrelated individuals

hyperplasia
    abnormally high cell growth and division

hypoplasia
    abnormally low cell growth and division

intermittent symptom
    symptom that occurs periodically

latency
    virus that remains in the body for a long period of time but only causes intermittent symptoms

lysis
    bursting of a cell

lytic cycle
      type of virus replication in which virions are released through lysis, or
      bursting, of the cell

lysogenic cycle
      type of virus replication in which the viral genome is incorporated into
      the genome of the host cell

oncogenic virus
      virus that has the ability to cause cancer

permissive
      cell type that is able to support productive replication of a virus

productive
      viral infection that leads to the production of new virions

prophage
      phage DNA that is incorporated into the host cell genome

vertical transmission
      transmission of disease from parent to offspring

Prevention and Treatment of Viral Infections

By the end of this section, you will be able to:

- Identify major viral illnesses that affect humans
- Compare vaccinations and anti-viral drugs as medical approaches to viruses

Viruses cause a variety of diseases in animals, including humans, ranging from the common cold to potentially fatal illnesses like meningitis ([link]). These diseases can be treated by antiviral drugs or by vaccines, but some viruses, such as HIV, are capable of both avoiding the immune response and mutating to become resistant to antiviral drugs.
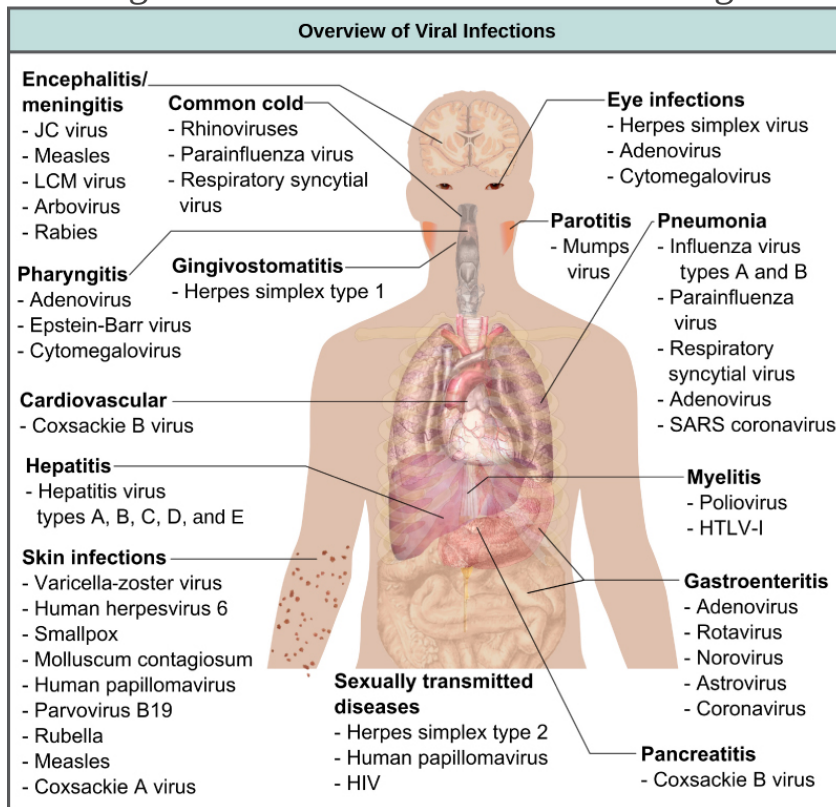
Viruses can cause dozens of ailments in humans, ranging from mild illnesses to serious diseases. (credit: modification of work by Mikael Häggström)

Vaccines for Prevention

While we do have limited numbers of effective antiviral drugs, such as those used to treat HIV and influenza, the primary method of controlling viral disease is by vaccination, which is intended to prevent outbreaks by building immunity to a virus or virus family ([link]). **Vaccines** may be prepared using live viruses, killed viruses, or molecular subunits of the virus. The killed viral vaccines and subunit viruses are both incapable of causing disease.

Live viral vaccines are designed in the laboratory to cause few symptoms in recipients while giving them protective immunity against future infections. Polio was one disease that represented a milestone in the use of vaccines. Mass immunization campaigns in the 1950s (killed vaccine) and 1960s (live vaccine) significantly reduced the incidence of the disease, which caused muscle paralysis in children and generated a great amount of fear in the general population when regional epidemics occurred. The success of the polio vaccine paved the way for the routine dispensation of childhood vaccines against measles, mumps, rubella, chickenpox, and other diseases.

The danger of using live vaccines, which are usually more effective than killed vaccines, is the low but significant danger that these viruses will revert to their disease-causing form by **back mutations**. Live vaccines are usually made by **attenuating** (weakening) the "wild-type" (disease-causing) virus by growing it in the laboratory in tissues or at temperatures different from what the virus is accustomed to in the host. Adaptations to these new cells or temperatures induce mutations in the genomes of the virus, allowing it to grow better in the laboratory while inhibiting its ability to cause disease when reintroduced into conditions found in the host. These attenuated viruses thus still cause infection, but they do not grow very well, allowing the immune response to develop in time to prevent major disease. Back mutations occur when the vaccine undergoes mutations in the host such that it readapts to the host and can again cause disease, which can then be spread to other humans in an epidemic. This type of scenario happened as recently as 2007 in Nigeria where mutations in a polio vaccine led to an epidemic of polio in that country.

Some vaccines are in continuous development because certain viruses, such as influenza and HIV, have a high mutation rate compared to other viruses and normal host cells. With influenza, mutations in the surface molecules of the virus help the organism evade the protective immunity that may have been obtained in a previous influenza season, making it necessary for individuals to get vaccinated every year. Other viruses, such as those that cause the childhood diseases measles, mumps, and rubella, mutate so infrequently that the same vaccine is used year after year.

Vaccinations are designed to boost immunity to a virus to prevent infection. (credit: USACE Europe District)

Note:
Link to Learning

Watch this NOVA [video](#) to learn how microbiologists are attempting to replicate the deadly 1918 Spanish influenza virus so they can understand more about virology.

Vaccines and Anti-viral Drugs for Treatment

In some cases, vaccines can be used to treat an active viral infection. The concept behind this is that by giving the vaccine, immunity is boosted without adding more disease-causing virus. In the case of rabies, a fatal neurological disease transmitted via the saliva of rabies virus-infected animals, the progression of the disease from the time of the animal bite to the time it enters the central nervous system may be 2 weeks or longer. This is enough time to vaccinate an individual who suspects that they have been bitten by a rabid animal, and their boosted immune response is sufficient to prevent the virus from entering nervous tissue. Thus, the potentially fatal neurological consequences of the disease are averted, and the individual only has to recover from the infected bite. This approach is also being used for the treatment of Ebola, one of the fastest and most deadly viruses on earth. Transmitted by bats and great apes, this disease can cause death in 70–90 percent of infected humans within 2 weeks. Using newly developed vaccines that boost the immune response in this way, there is hope that affected individuals will be better able to control the virus, potentially saving a greater percentage of infected persons from a rapid and very painful death.

Another way of treating viral infections is the use of antiviral drugs. These drugs often have limited success in curing viral disease, but in many cases, they have been used to control and reduce symptoms for a wide variety of viral diseases. For most viruses, these drugs can inhibit the virus by

blocking the actions of one or more of its proteins. It is important that the targeted proteins be encoded by viral genes and that these molecules are not present in a healthy host cell. In this way, viral growth is inhibited without damaging the host. There are large numbers of antiviral drugs available to treat infections, some specific for a particular virus and others that can affect multiple viruses.

Antivirals have been developed to treat genital herpes (herpes simplex II) and influenza. For genital herpes, drugs such as acyclovir can reduce the number and duration of episodes of active viral disease, during which patients develop viral lesions in their skin cells. As the virus remains latent in nervous tissue of the body for life, this drug is not curative but can make the symptoms of the disease more manageable. For influenza, drugs like Tamiflu (oseltamivir) ([link]) can reduce the duration of "flu" symptoms by 1 or 2 days, but the drug does not prevent symptoms entirely. Tamiflu works by inhibiting an enzyme (viral neuraminidase) that allows new virions to leave their infected cells. Thus, Tamiflu inhibits the spread of virus from infected to uninfected cells. Other antiviral drugs, such as Ribavirin, have been used to treat a variety of viral infections, although its mechanism of action against certain viruses remains unclear.
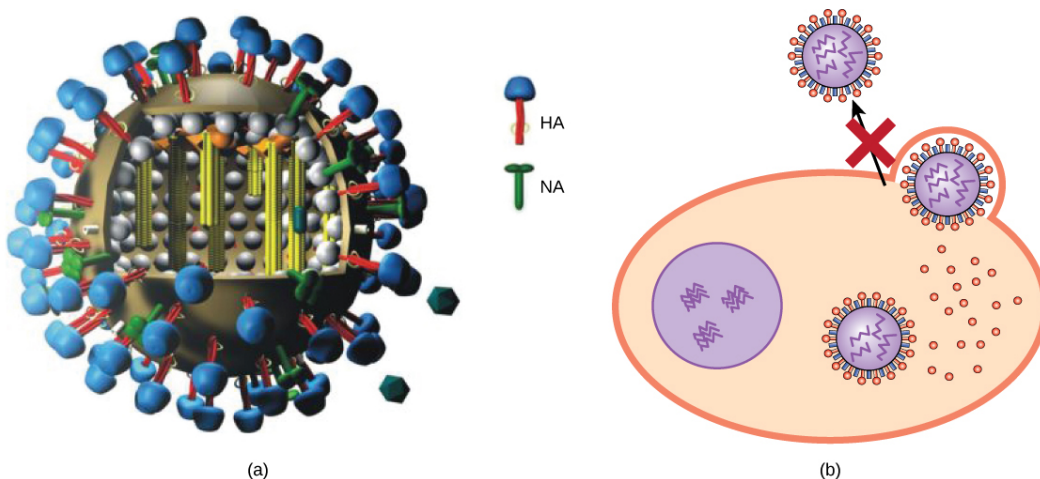
(a) Tamiflu inhibits a viral enzyme called neuraminidase (NA) found in the influenza viral envelope. (b) Neuraminidase cleaves the connection between viral

hemagglutinin (HA), also found in the viral envelope, and glycoproteins on the host cell surface. Inhibition of neuraminidase prevents the virus from detaching from the host cell, thereby blocking further infection. (credit a: modification of work by M. Eickmann)

By far, the most successful use of antivirals has been in the treatment of the retrovirus HIV, which causes a disease that, if untreated, is usually fatal within 10–12 years after infection. Anti-HIV drugs have been able to control viral replication to the point that individuals receiving these drugs survive for a significantly longer time than the untreated.

Anti-HIV drugs inhibit viral replication at many different phases of the HIV replicative cycle ([link]). Drugs have been developed that inhibit the fusion of the HIV viral envelope with the plasma membrane of the host cell (fusion inhibitors), the conversion of its RNA genome into double-stranded DNA (reverse transcriptase inhibitors), the integration of the viral DNA into the host genome (integrase inhibitors), and the processing of viral proteins (protease inhibitors).
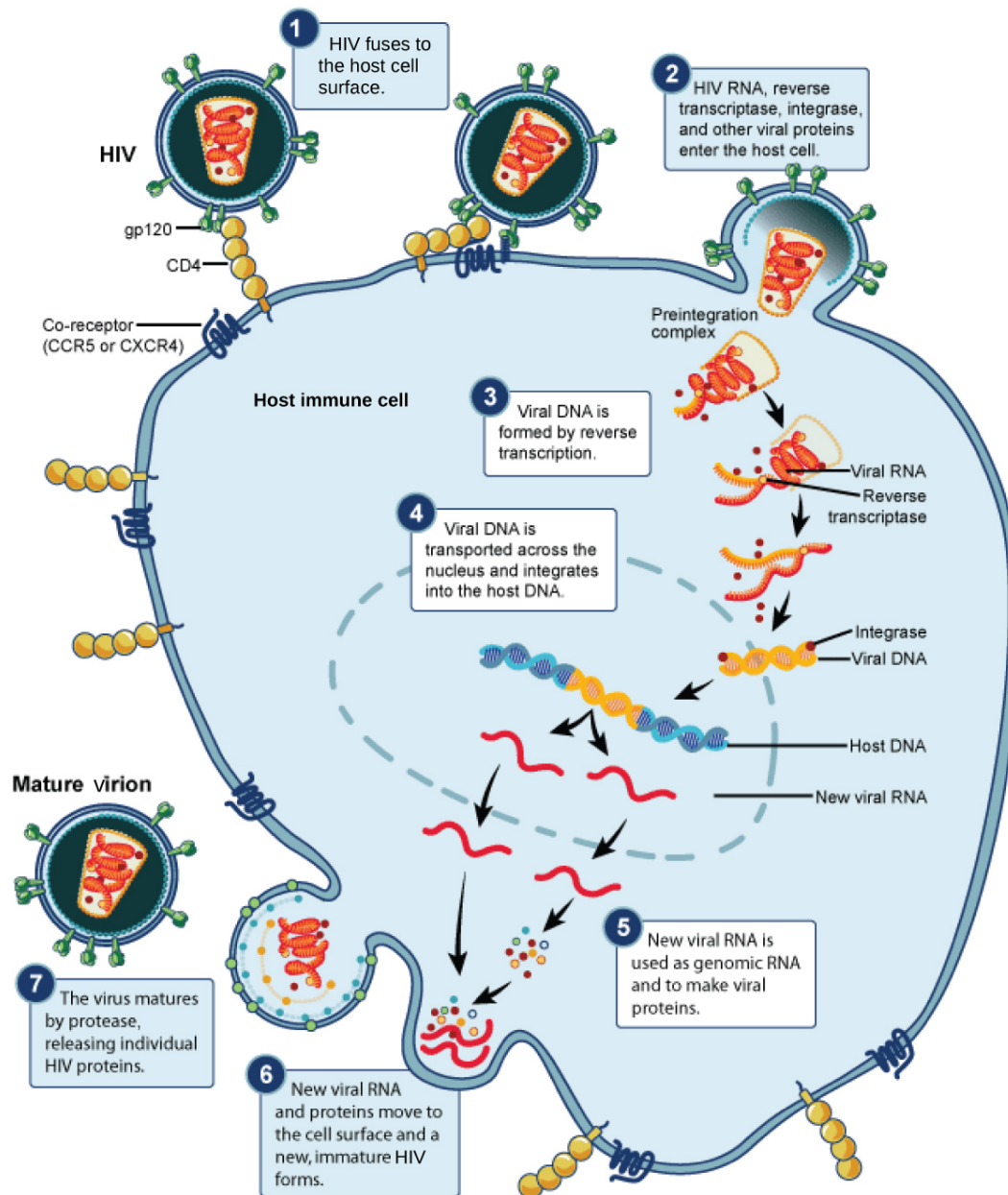
HIV, an enveloped, icosahedral virus, attaches to the CD4 receptor of an immune cell and fuses with the cell membrane. Viral contents are released into the cell, where viral enzymes convert the single-stranded RNA genome into DNA and incorporate it into the host genome. (credit: NIAID, NIH)

When any of these drugs are used individually, the high mutation rate of the virus allows it to easily and rapidly develop resistance to the drug, limiting the drug's effectiveness. The breakthrough in the treatment of HIV was the development of HAART, highly active anti-retroviral therapy, which involves a mixture of different drugs, sometimes called a drug "cocktail." By attacking the virus at different stages of its replicative cycle, it is much more difficult for the virus to develop resistance to multiple drugs at the same time. Still, even with the use of combination HAART therapy, there is concern that, over time, the virus will develop resistance to this therapy. Thus, new anti-HIV drugs are constantly being developed with the hope of continuing the battle against this highly fatal virus.

Note:
Everyday Connection
Applied Virology
The study of viruses has led to the development of a variety of new ways to treat non-viral diseases. Viruses have been used in **gene therapy**. Gene therapy is used to treat genetic diseases such as severe combined immunodeficiency (SCID), a heritable, recessive disease in which children are born with severely compromised immune systems. One common type of SCID is due to the lack of an enzyme, adenosine deaminase (ADA), which breaks down purine bases. To treat this disease by gene therapy, bone marrow cells are taken from a SCID patient and the ADA gene is inserted. This is where viruses come in, and their use relies on their ability to penetrate living cells and bring genes in with them. Viruses such as adenovirus, an upper respiratory human virus, are modified by the addition of the ADA gene, and the virus then transports this gene into the cell. The modified cells, now capable of making ADA, are then given back to the patients in the hope of curing them. Gene therapy using viruses as carrier of genes (viral vectors), although still experimental, holds promise for the treatment of many genetic diseases. Still, many technological problems need to be solved for this approach to be a viable method for treating genetic disease.
Another medical use for viruses relies on their specificity and ability to kill the cells they infect. **Oncolytic viruses** are engineered in the laboratory

specifically to attack and kill cancer cells. A genetically modified adenovirus known as H101 has been used since 2005 in clinical trials in China to treat head and neck cancers. The results have been promising, with a greater short-term response rate to the combination of chemotherapy and viral therapy than to chemotherapy treatment alone. This ongoing research may herald the beginning of a new age of cancer therapy, where viruses are engineered to find and specifically kill cancer cells, regardless of where in the body they may have spread.

A third use of viruses in medicine relies on their specificity and involves using bacteriophages in the treatment of bacterial infections. Bacterial diseases have been treated with antibiotics since the 1940s. However, over time, many bacteria have developed resistance to antibiotics. A good example is methicillin-resistant *Staphylococcus aureus* (MRSA, pronounced "mersa"), an infection commonly acquired in hospitals. This bacterium is resistant to a variety of antibiotics, making it difficult to treat. The use of bacteriophages specific for such bacteria would bypass their resistance to antibiotics and specifically kill them. Although **phage therapy** is in use in the Republic of Georgia to treat antibiotic-resistant bacteria, its use to treat human diseases has not been approved in most countries. However, the safety of the treatment was confirmed in the United States when the U.S. Food and Drug Administration approved spraying meats with bacteriophages to destroy the food pathogen *Listeria*. As more and more antibiotic-resistant strains of bacteria evolve, the use of bacteriophages might be a potential solution to the problem, and the development of phage therapy is of much interest to researchers worldwide.

Section Summary

Viruses cause a variety of diseases in humans. Many of these diseases can be prevented by the use of viral vaccines, which stimulate protective immunity against the virus without causing major disease. Viral vaccines may also be used in active viral infections, boosting the ability of the immune system to control or destroy the virus. A series of antiviral drugs that target enzymes and other protein products of viral genes have been

developed and used with mixed success. Combinations of anti-HIV drugs have been used to effectively control the virus, extending the lifespans of infected individuals. Viruses have many uses in medicines, such as in the treatment of genetic disorders, cancer, and bacterial infections.

Review Questions

Exercise:

Problem:

Which of the following is NOT used to treat active viral disease?

a. vaccines
b. antiviral drugs
c. antibiotics
d. phage therapy

Solution:

C

Exercise:

Problem: Vaccines _____.

a. are similar to viroids
b. are only needed once
c. kill viruses
d. stimulate an immune response

Solution:

D

Free Response

Exercise:

Problem:

Why is immunization after being bitten by a rabid animal so effective and why aren't people vaccinated for rabies like dogs and cats are?

Solution:

Rabies vaccine works after a bite because it takes week for the virus to travel from the site of the bite to the central nervous system, where the most severe symptoms of the disease occur. Adults are not routinely vaccinated for rabies for two reasons: first, because the routine vaccination of domestic animals makes it unlikely that humans will contract rabies from an animal bite; second, if one is bitten by a wild animal or a domestic animal that one cannot confirm has been immunized, there is still time to give the vaccine and avoid the often fatal consequences of the disease.

Glossary

attenuation
    weakening of a virus during vaccine development

back mutation
    when a live virus vaccine reverts back to it disease-causing phenotype

gene therapy
    treatment of genetic disease by adding genes, using viruses to carry the new genes inside the cell

oncolytic virus
    virus engineered to specifically infect and kill cancer cells

phage therapy
    treatment of bacterial diseases using bacteriophages specific to a particular bacterium

vaccine
    weakened solution of virus components, viruses, or other agents that produce an immune response

Other Acellular Entities: Prions and Viroids
By the end of this section, you will be able to:

- Describe prions and their basic properties
- Define viroids and their targets of infection

Prions and viroids are **pathogens** (agents with the ability to cause disease) that have simpler structures than viruses but, in the case of prions, still can produce deadly diseases.

Prions

Prions, so-called because they are proteinaceous, are infectious particles—smaller than viruses—that contain no nucleic acids (neither DNA nor RNA). Historically, the idea of an infectious agent that did not use nucleic acids was considered impossible, but pioneering work by Nobel Prize-winning biologist Stanley Prusiner has convinced the majority of biologists that such agents do indeed exist.

Fatal neurodegenerative diseases, such as kuru in humans and bovine spongiform encephalopathy (BSE) in cattle (commonly known as "mad cow disease") were shown to be transmitted by prions. The disease was spread by the consumption of meat, nervous tissue, or internal organs between members of the same species. Kuru, native to humans in Papua New Guinea, was spread from human to human via ritualistic cannibalism. BSE, originally detected in the United Kingdom, was spread between cattle by the practice of including cattle nervous tissue in feed for other cattle. Individuals with kuru and BSE show symptoms of loss of motor control and unusual behaviors, such as uncontrolled bursts of laughter with kuru, followed by death. Kuru was controlled by inducing the population to abandon its ritualistic cannibalism.

On the other hand, BSE was initially thought to only affect cattle. Cattle dying of the disease were shown to have developed lesions or "holes" in the brain, causing the brain tissue to resemble a sponge. Later on in the outbreak, however, it was shown that a similar encephalopathy in humans known as variant Creutzfeldt-Jakob disease (CJD) could be acquired from

eating beef from animals with BSE, sparking bans by various countries on the importation of British beef and causing considerable economic damage to the British beef industry ([link]). BSE still exists in various areas, and although a rare disease, individuals that acquire CJD are difficult to treat. The disease can be spread from human to human by blood, so many countries have banned blood donation from regions associated with BSE.

The cause of spongiform encephalopathies, such as kuru and BSE, is an infectious structural variant of a normal cellular protein called PrP (prion protein). It is this variant that constitutes the prion particle. PrP exists in two forms, **PrP^C**, the normal form of the protein, and **PrP^{SC}**, the infectious form. Once introduced into the body, the PrP^{SC} contained within the prion binds to PrP^C and converts it to PrP^{SC}. This leads to an exponential increase of the PrP^{SC} protein, which aggregates. PrP^{SC} is folded abnormally, and the resulting conformation (shape) is directly responsible for the lesions seen in the brains of infected cattle. Thus, although not without some detractors among scientists, the prion seems likely to be an entirely new form of infectious agent, the first one found whose transmission is not reliant upon genes made of DNA or RNA.

(a) Endogenous normal prion protein (PrP^C) is converted into the disease-causing form (PrP^{SC}) when it encounters this variant form of the protein. PrP^{SC} may arise spontaneously in brain tissue, especially if a mutant form of the protein is present, or it
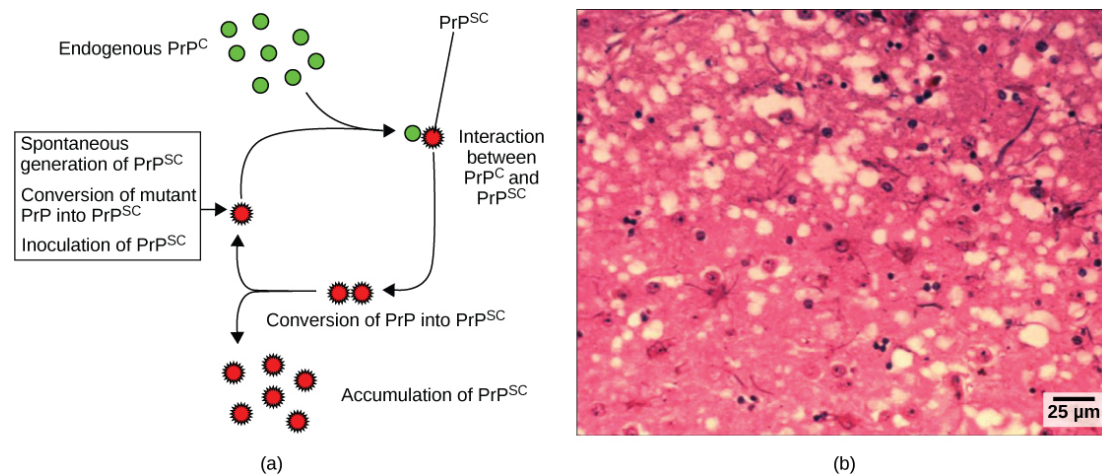
may occur via the spread of misfolded prions consumed in food into brain tissue. (b) This prion-infected brain tissue, visualized using light microscopy, shows the vacuoles that give it a spongy texture, typical of transmissible spongiform encephalopathies. (credit b: modification of work by Dr. Al Jenny, USDA APHIS; scale-bar data from Matt Russell)

Viroids

Viroids are plant pathogens: small, single-stranded, circular RNA particles that are much simpler than a virus. They do not have a capsid or outer envelope, but like viruses can reproduce only within a host cell. Viroids do not, however, manufacture any proteins, and they only produce a single, specific RNA molecule. Human diseases caused by viroids have yet to be identified.

Viroids are known to infect plants ([link]) and are responsible for crop failures and the loss of millions of dollars in agricultural revenue each year. Some of the plants they infect include potatoes, cucumbers, tomatoes, chrysanthemums, avocados, and coconut palms.

These potatoes have been infected by the potato spindle tuber viroid (PSTV), which is typically spread when infected knives are used to cut healthy potatoes, which are then planted. (credit: Pamela Roberts, University of Florida Institute of Food and Agricultural Sciences, USDA ARS)

Note:
Career Connection
Virologist
Virology is the study of viruses, and a virologist is an individual trained in this discipline. Training in virology can lead to many different career paths. Virologists are actively involved in academic research and teaching in colleges and medical schools. Some virologists treat patients or are involved in the generation and production of vaccines. They might participate in epidemiologic studies ([link]) or become science writers, to name just a few possible careers.

This virologist is engaged in fieldwork, sampling eggs from this nest for avian influenza. (credit: Don Becker, USGS EROS, U.S. Fish and Wildlife Service)

If you think you may be interested in a career in virology, find a mentor in the field. Many large medical centers have departments of virology, and smaller hospitals usually have virology labs within their microbiology departments. Volunteer in a virology lab for a semester or work in one over the summer. Discussing the profession and getting a first-hand look at the work will help you decide whether a career in virology is right for you. The American Society of Virology's website is a good resource for information regarding training and careers in virology.

Section Summary

Prions are infectious agents that consist of protein, but no DNA or RNA, and seem to produce their deadly effects by duplicating their shapes and accumulating in tissues. They are thought to contribute to several progressive brain disorders, including mad cow disease and Creutzfeldt-Jakob disease. Viroids are single-stranded RNA pathogens that infect plants. Their presence can have a severe impact on the agriculture industry.

Review Questions

Exercise:

Problem: Which of the following is not associated with prions?

    a. replicating shapes
    b. mad cow disease
    c. DNA
    d. toxic proteins

Solution:

C

Exercise:

Problem: Which statement is true of viroids?

    a. They are single-stranded RNA particles.
    b. They reproduce only outside of the cell.
    c. They produce proteins.
    d. They affect both plants and animals.

Solution:

A

Free Response

Exercise:

Problem:

Prions are responsible for variant Creutzfeldt-Jakob Disease, which has resulted in over 100 human deaths in Great Britain during the last 10 years. How do humans obtain this disease?

Solution:

This prion-based disease is transmitted through human consumption of infected meat.

Exercise:

Problem: How are viroids like viruses?

Solution:

They both replicate in a cell, and they both contain nucleic acid.

Glossary

pathogen
    agent with the ability to cause disease

prion
    infectious particle that consists of proteins that replicate without DNA or RNA

PrP^c
    normal prion protein

PrP^{sc}
    infectious form of a prion protein

viroid
	plant pathogen that produces only a single, specific RNA

Introduction
class="introduction"

Protists range from the microscopic, single-celled (a) *Acanthocystis turfacea* and the (b) ciliate *Tetrahymena thermophila*, both visualized here using light microscopy, to the enormous, multicellular (c) kelps (Chromalveolata) that extend for hundreds of feet in underwater "forests." (credit a: modification of work by Yuiuji Tsukii; credit b: modification of work by Richard Robinson, Public Library of Science; credit c: modification of work by Kip Evans, NOAA; scale-bar data

(a) (b) (c)
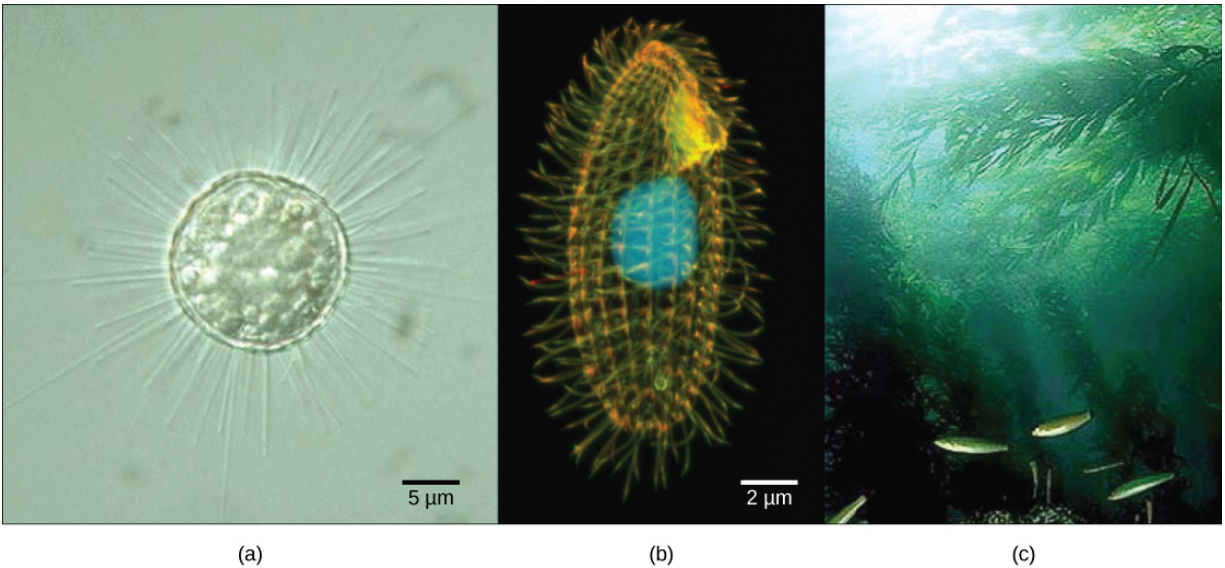
Humans have been familiar with macroscopic organisms (organisms big enough to see with the unaided eye) since before there was a written history, and it is likely that most cultures distinguished between animals and land plants, and most probably included the macroscopic fungi as plants. Therefore, it became an interesting challenge to deal with the world of microorganisms once microscopes were developed a few centuries ago. Many different naming schemes were used over the last couple of centuries, but it has become the most common practice to refer to eukaryotes that are not land plants, animals, or fungi as protists.

This name was first suggested by Ernst Haeckel in the late nineteenth century. It has been applied in many contexts and has been formally used to represent a kingdom-level taxon called Protista. However, many modern systematists (biologists who study the relationships among organisms) are beginning to shy away from the idea of formal ranks such as kingdom and phylum. Instead, they are naming taxa as groups of organisms thought to include all the descendants of a last common ancestor (monophyletic group). During the past two decades, the field of molecular genetics has demonstrated that some protists are more related to animals, plants, or fungi than they are to other protists. Therefore, not including animals, plants and fungi make the kingdom Protista a paraphyletic group, or one that does not

include all descendents of its common ancestor. For this reason, protist lineages originally classified into the kingdom Protista continue to be examined and debated. In the meantime, the term "protist" still is used informally to describe this tremendously diverse group of eukaryotes.

Most protists are microscopic, unicellular organisms that are abundant in soil, freshwater, brackish, and marine environments. They are also common in the digestive tracts of animals and in the vascular tissues of plants. Others invade the cells of other protists, animals, and plants. Not all protists are microscopic. Some have huge, macroscopic cells, such as the plasmodia (giant amoebae) of myxomycete slime molds or the marine green alga *Caulerpa*, which can have single cells that can be several meters in size. Some protists are multicellular, such as the red, green, and brown seaweeds. It is among the protists that one finds the wealth of ways that organisms can grow.

Groups of Protists
By the end of this section, you will be able to:

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called convergent evolution, is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six "supergroups" that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor ([link]). The supergroups are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

Eukaryotic Supergroups

Diplomonads	Excavata
Parabasalids	
Euglenozoans	
Dinoflagellates	Chromalveolata
Apicomplexans	
Ciliates	
Diatoms	
Golden algae	
Brown algae	
Oomycetes	
Cercozoans	Rhizaria
Forams	
Radiolarians	
Red algae	Archaeplastida
Chlorophytes (green algae)	
Charophytes (green algae)	
Land plants	
Slime molds	Amoebozoa
Gymnamoebas	
Entamoebas	
Nucleariids	Opisthokonta
Fungi	
Choanoflagellates	
Animals	

Alveolates, Stramenopiles, Common eukaryotic ancestor

This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove "excavated" from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia* ([link]). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called **mitosomes**, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.

The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell)

Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called **hydrogenosomes** because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes

trichamoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the **kinetoplast**, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.
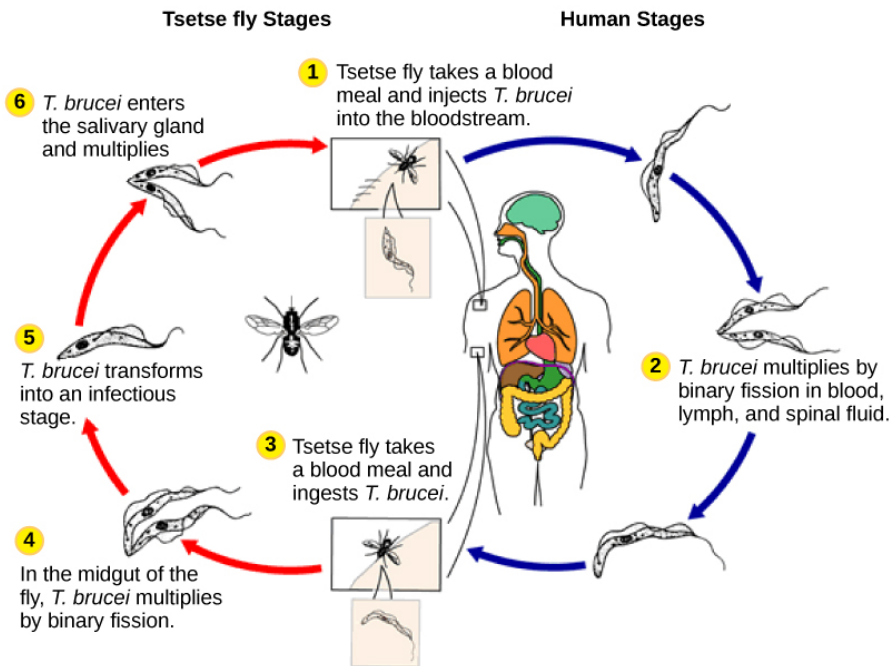
Trypanosoma brucei, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Note:
Link to Learning

Watch this video to see *T. brucei* swimming.
https://www.openstaxcollege.org/l/T_brucei

Chromalveolata

Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether. Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexians, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate ([link]). Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of **plankton**, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.
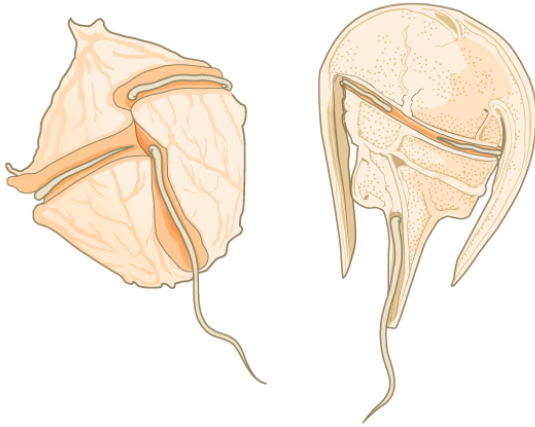
The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

Some dinoflagellates generate light, called **bioluminescence**, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color ([link]). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.

Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: "catalano82"/Flickr)

The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex ([link]). The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.
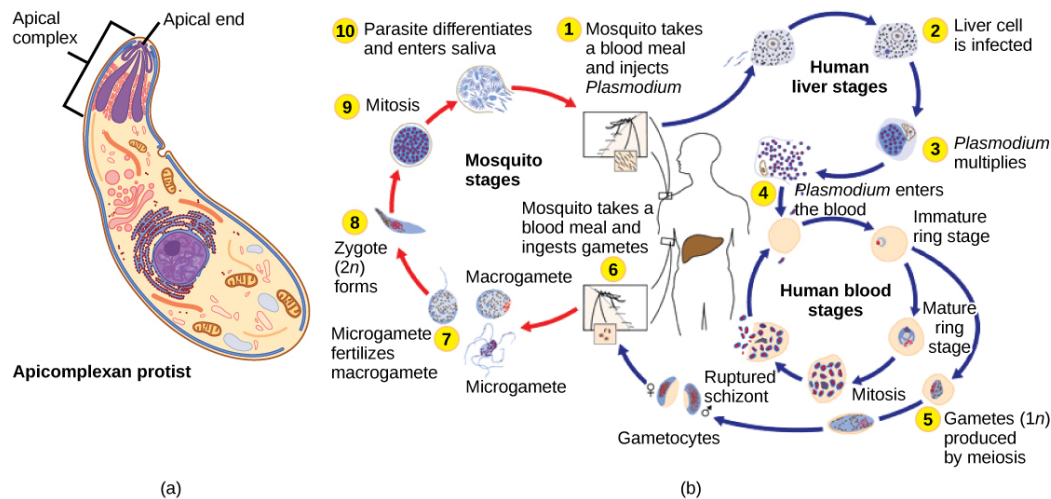
(a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria ([link]). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses **contractile vacuoles**, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.
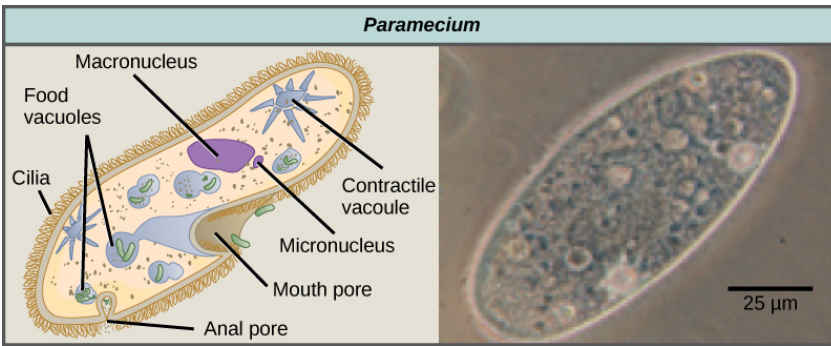
Paramecium has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt Russell)

Note:
Link to Learning

Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.
https://www.openstaxcollege.org/l/paramecium

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the

macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge ([link]). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

Note:
Art Connection

Sexual Reproduction in *Paramecium*

Macronucleus

Cytoplasmic bridge

Micronucleus

1 Two different mating types form a cytoplasmic bridge.

2 Meiosis produces four haploid micronuclei, three of which disintegrate.

3 Each remaining micronucleus divides by mitosis.

4 The conjugate pair swaps micronuclei.

5 The haploid micronuclei fuse, forming a diploid micronucleus.

6 The micronucleus undergoes three rounds of mitosis, producing eight micronuclei.

7 The original macronucleus disintegrates, and four of the micronuclei become macronuclei.

8 Two rounds of cell division produce four daughter cells.

25 µm

The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work by Ian Sutton; scale-bar data from Matt Russell)

Which of the following statements about *Paramecium* sexual reproduction is false?

    a. The macronuclei are derived from micronuclei.
    b. Both mitosis and meiosis occur during sexual reproduction.
    c. The conjugate pair swaps macronucleii.
    d. Each parent produces four daughter cells.

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or "hairy," flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections ([link]). Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.
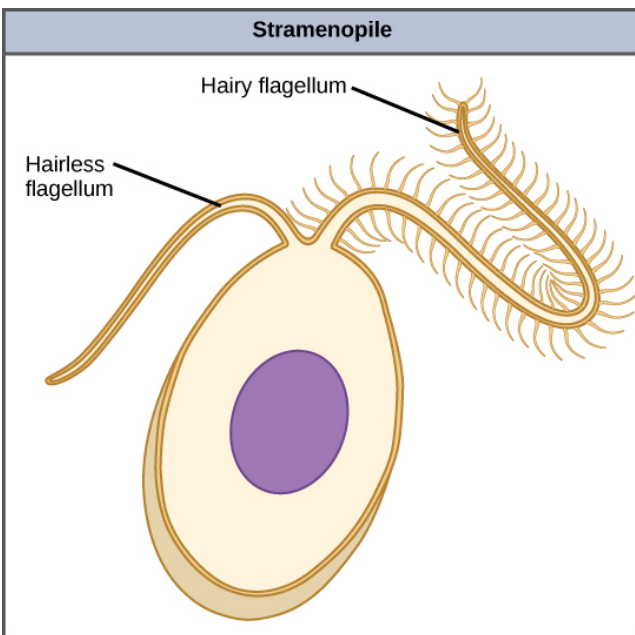
This stramenopile cell has a single

hairy flagellum and a secondary
smooth flagellum.

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles ([link]). These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell, called a **raphe**. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.
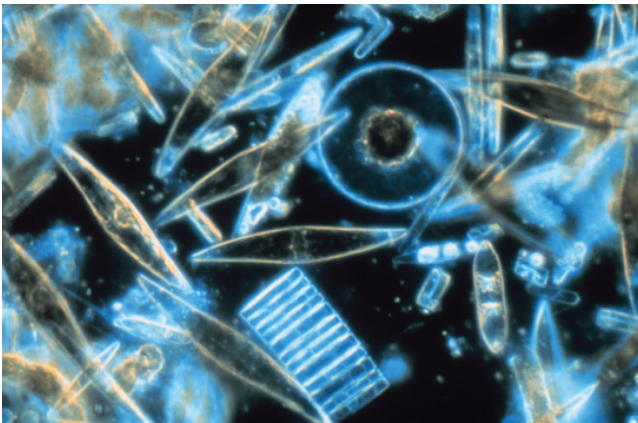
Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 μm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the **biological carbon pump**, because carbon is "pumped" to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form ([link]). Certain

other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

Laminaria Life Cycle
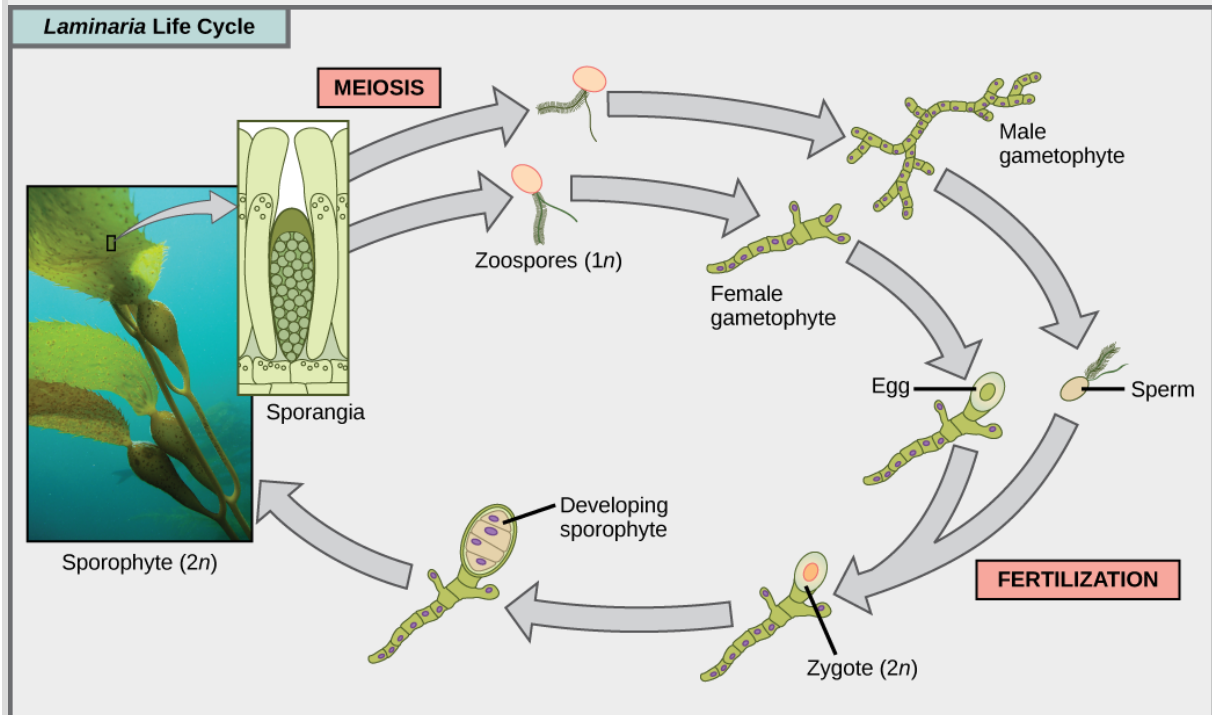
Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit "laminaria photograph": modification of work by Claire Fackler, CINMS, NOAA Photo Library)

Which of the following statements about the *Laminaria* life cycle is false?

  a. $1n$ zoospores form in the sporangia.
  b. The sporophyte is the $2n$ plant.
  c. The gametophyte is diploid.
  d. Both the gametophyte and sporophyte stages are multicellular.

The water molds, oomycetes ("egg fungus"), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms ([link]). Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.

A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia ([link]). Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called **cytoplasmic streaming**, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.
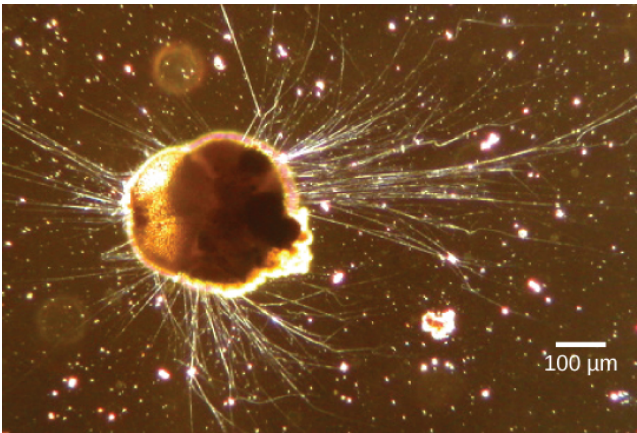
Ammonia tepida, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia. (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

Note:
Link to Learning

Take a look at this video to see cytoplasmic streaming in a green alga. https://www.openstaxcollege.org/l/chara_corallina

Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails ([link]). As a group, the forams exhibit porous shells, called **tests** that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.
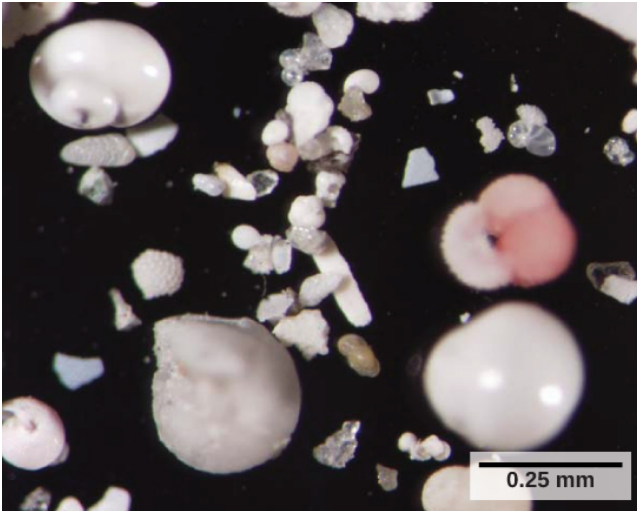
These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER)

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry ([link]). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.
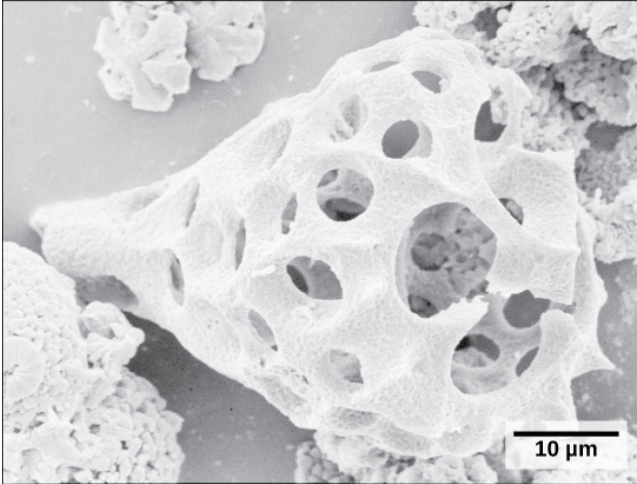
This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle

is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism ([link]). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.
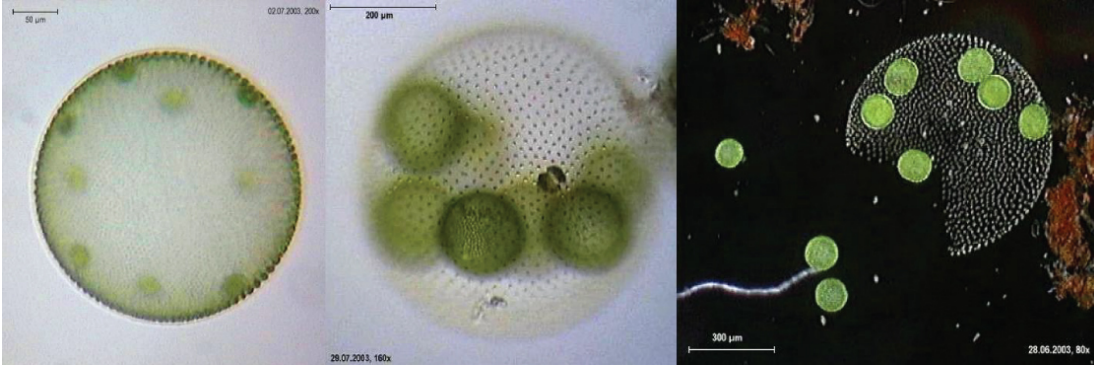
Volvox aureus is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters ([link]). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.

Caulerpa taxifolia is a chlorophyte consisting of a single cell

containing potentially thousands
of nuclei. (credit: NOAA)

Amoebozoa

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba ([link]). The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.
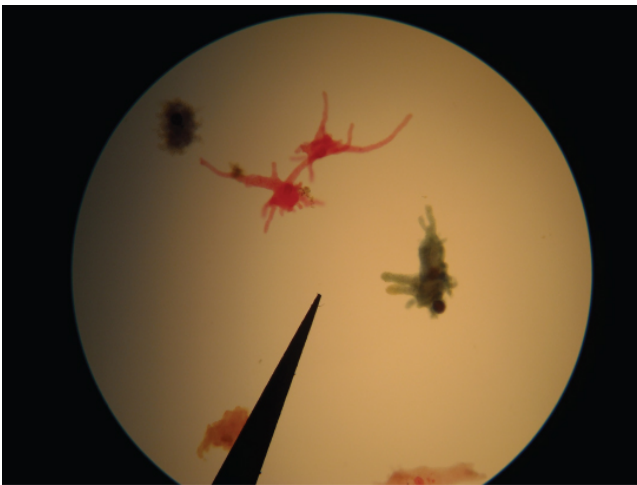
Amoebae with tubular and lobe-
shaped pseudopodia are seen
under a microscope. These isolates
would be morphologically
classified as amoebozoans.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage ([link]). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

Plasmodial Slime Mold Life Cycle

Germination gives rise to cells that can convert between amoeboid and flagelated forms.

Spores (1*n*)

Meiosis within the sporangium results in haploid spores.

Sporangium

Stalk

Amoeboid

Flagellated

Fertilization by fusion of either cell type results in a 2*n* zygote.

The plasmodium matures and sporangia form.

Mature plasmodium

Zygote (2*n*)

Mitosis without cytokinesis results in a single-celled multinucleate mass called a plasmodium

Feeding plasmodium

The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant ([link]). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One

representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

Cellular Slime Mold Life Cycle

Germination gives rise to amoeboid cells.

The spores disperse.

Spore (1*n*)

Mitosis and Meiosis

Asexual reproduction

Solitary amoebas (1*n*)

Sexual reproduction

Zygote (2*n*)

Fertilization

Mitosis without cytokinesis results in multiple solitary amoebas that may aggregate. The aggregated amoebas are able to migrate.

Aggregated amoebas

Fruiting body

Stalk

Cells migrate up the stalk and form spores.

A stalk forms with a fruiting body at the top.

Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

Note:
Link to Learning

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

The Mesomycetozoa form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood. These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology.

Section Summary

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Amoebozoa, and Opisthokonta. The goal of this

classification scheme is to create clusters of species that all are derived from a common ancestor. At present, the monophyly of some of the supergroups are better supported by genetic data than others. Although tremendous variation exists within the supergroups, commonalities at the morphological, physiological, and ecological levels can be identified.

Art Connections

Exercise:

  Problem:

  [link] Which of the following statements about *Paramecium* sexual reproduction is false?

   a. The macronuclei are derived from micronuclei.
   b. Both mitosis and meiosis occur during sexual reproduction.
   c. The conjugate pair swaps macronuclei.
   d. Each parent produces four daughter cells.

  Solution:

  [link] C

Exercise:

  Problem:

  [link] Which of the following statements about the *Laminaria* life cycle is false?

   a. 1*n* zoospores form in the sporangia.
   b. The sporophyte is the *2n* plant.
   c. The gametophyte is diploid.
   d. Both the gametophyte and sporophyte stages are multicellular.

  Solution:

C

Review Questions

Exercise:

Problem:

Which protist group exhibits mitochondrial remnants with reduced functionality?

    a. slime molds
    b. diatoms
    c. parabasalids
    d. dinoflagellates

Solution:

C

Exercise:

Problem:

Conjugation between two *Paramecia* produces _____ total daughter cells.

    a. 2
    b. 4
    c. 8
    d. 16

Solution:

C

Exercise:

Problem: What is the function of the raphe in diatoms?

   a. locomotion
   b. defense
   c. capturing food
   d. photosynthesis

Solution:

A

Exercise:

Problem:

What genus of protists appears to contradict the statement that unicellularity restricts cell size?

   a. *Dictyostelium*
   b. *Ulva*
   c. *Plasmodium*
   d. *Caulerpa*

Solution:

D

Free Response

Exercise:

Problem:

The chlorophyte (green algae) genera *Ulva* and *Caulerpa* both have macroscopic leaf-like and stem-like structures, but only *Ulva* species are considered truly multicellular. Explain why.

Solution:

Unlike *Ulva*, protists in the genus *Caulerpa* actually are large, multinucleate, single cells. Because these organisms undergo mitosis without cytokinesis and lack cytoplasmic divisions, they cannot be considered truly multicellular.

Exercise:

Problem:

Why might a light-sensing eyespot be ineffective for an obligate saprobe? Suggest an alternative organ for a saprobic protist.

Solution:

By definition, an obligate saprobe lacks the ability to perform photosynthesis, so it cannot directly obtain nutrition by searching for light. Instead, a chemotactic mechanism that senses the odors released during decay might be a more effective sensing organ for a saprobe.

Glossary

biological carbon pump
> process by which inorganic carbon is fixed by photosynthetic species that then die and fall to the sea floor where they cannot be reached by saprobes and their carbon dioxide consumption cannot be returned to the atmosphere

bioluminescence
> generation and emission of light by an organism, as in dinoflagellates

contractile vacuole
> vesicle that fills with water (as it enters the cell by osmosis) and then contracts to squeeze water from the cell; an osmoregulatory vesicle

cytoplasmic streaming

movement of cytoplasm into an extended pseudopod such that the entire cell is transported to the site of the pseudopod

hydrogenosome
    organelle carried by parabasalids (Excavata) that functions anaerobically and outputs hydrogen gas as a byproduct; likely evolved from mitochondria

kinetoplast
    mass of DNA carried within the single, oversized mitochondrion, characteristic of kinetoplastids (phylum: Euglenozoa)

mitosome
    nonfunctional organelle carried in the cells of diplomonads (Excavata) that likely evolved from a mitochondrion

plankton
    diverse group of mostly microscopic organisms that drift in marine and freshwater systems and serve as a food source for larger aquatic organisms

raphe
    slit in the silica shell of diatoms through which the protist secretes a stream of mucopolysaccharides for locomotion and attachment to substrates

test
    porous shell of a foram that is built from various organic materials and typically hardened with calcium carbonate

Ecology of Protists
By the end of this section, you will be able to:

- Describe the role that protists play in the ecosystem
- Describe important pathogenic species of protists

Protists function in various ecological niches. Whereas some protist species are essential components of the food chain and generators of biomass, others function in the decomposition of organic materials. Still other protists are dangerous human pathogens or causative agents of devastating plant diseases.

Primary Producers/Food Sources

Protists are essential sources of nutrition for many other organisms. In some cases, as in plankton, protists are consumed directly. Alternatively, photosynthetic protists serve as producers of nutrition for other organisms. For instance, photosynthetic dinoflagellates called zooxanthellae use sunlight to fix inorganic carbon. In this symbiotic relationship, these protists provide nutrients for coral polyps ([link]) that house them, giving corals a boost of energy to secrete a calcium carbonate skeleton. In turn, the corals provide the protist with a protected environment and the compounds needed for photosynthesis. This type of symbiotic relationship is important in nutrient-poor environments. Without dinoflagellate symbionts, corals lose algal pigments in a process called coral bleaching, and they eventually die. This explains why reef-building corals do not reside in waters deeper than 20 meters: insufficient light reaches those depths for dinoflagellates to photosynthesize.

Coral polyps obtain nutrition through a symbiotic relationship with dinoflagellates.

The protists themselves and their products of photosynthesis are essential—directly or indirectly—to the survival of organisms ranging from bacteria to mammals ([link]). As primary producers, protists feed a large proportion of the world's aquatic species. (On land, terrestrial plants serve as primary producers.) In fact, approximately one-quarter of the world's photosynthesis is conducted by protists, particularly dinoflagellates, diatoms, and multicellular algae.

Virtually all aquatic organisms depend directly or indirectly on protists for food. (credit "mollusks": modification of work by Craig Stihler, USFWS; credit "crab": modification of work by David Berkowitz; credit "dolphin": modification of work by Mike Baird; credit "fish": modification of work by Tim Sheerman-Chase; credit "penguin": modification of work by Aaron Logan)

Protists do not create food sources only for sea-dwelling organisms. For instance, certain anaerobic parabasalid species exist in the digestive tracts of termites and wood-eating cockroaches, where they contribute an essential step in the digestion of cellulose ingested by these insects as they bore through wood.

Human Pathogens

A pathogen is anything that causes disease. Parasites live in or on an organism and harm the organism. A significant number of protists are pathogenic parasites that must infect other organisms to survive and propagate. Protist parasites include the causative agents of malaria, African sleeping sickness, and waterborne gastroenteritis in humans. Other protist pathogens prey on plants, effecting massive destruction of food crops.

Plasmodium Species

Members of the genus *Plasmodium* must colonize both a mosquito and a vertebrate to complete their life cycle. In vertebrates, the parasite develops in liver cells and goes on to infect red blood cells, bursting from and destroying the blood cells with each asexual replication cycle ([link]). Of the four *Plasmodium* species known to infect humans, *P. falciparum* accounts for 50 percent of all malaria cases and is the primary cause of disease-related fatalities in tropical regions of the world. In 2010, it was estimated that malaria caused between one-half and one million deaths, mostly in African children. During the course of malaria, *P. falciparum* can infect and destroy more than one-half of a human's circulating blood cells, leading to severe anemia. In response to waste products released as the parasites burst from infected blood cells, the host immune system mounts a massive inflammatory response with episodes of delirium-inducing fever as parasites lyse red blood cells, spilling parasite waste into the bloodstream. *P. falciparum* is transmitted to humans by the African malaria mosquito, *Anopheles gambiae*. Techniques to kill, sterilize, or avoid exposure to this highly aggressive mosquito species are crucial to malaria control.
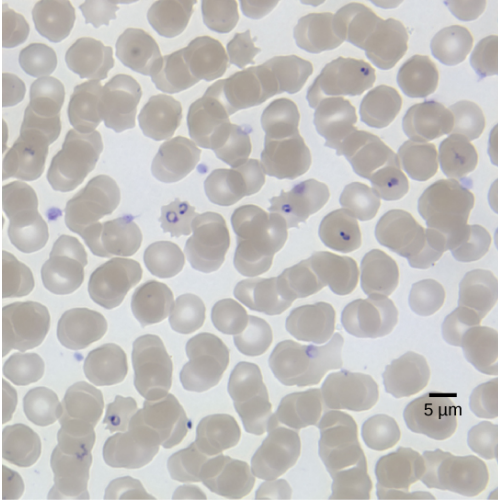
Red blood cells are shown to be infected with *P. falciparum*, the causative agent of malaria. In this light microscopic image taken using a 100× oil immersion lens, the ring-shaped *P. falciparum* stains purple. (credit: modification of work by Michael Zahniser; scale-bar data from Matt Russell)

Note:
Link to Learning

This [movie](#) depicts the pathogenesis of *Plasmodium falciparum*, the causative agent of malaria.

Trypanosomes

Trypanosoma brucei, the parasite that is responsible for African sleeping sickness, confounds the human immune system by changing its thick layer of surface glycoproteins with each infectious cycle ([link]). The glycoproteins are identified by the immune system as foreign antigens, and a specific antibody defense is mounted against the parasite. However, *T. brucei* has thousands of possible antigens, and with each subsequent generation, the protist switches to a glycoprotein coating with a different molecular structure. In this way, *T. brucei* is capable of replicating continuously without the immune system ever succeeding in clearing the parasite. Without treatment, *T. brucei* crosses the blood-brain barrier and infects the central nervous system, causing the patient to lapse into a coma and eventually die. During epidemic periods, mortality from the disease can be high. Greater surveillance and control measures lead to a reduction in reported cases; some of the lowest numbers reported in 50 years (fewer than 10,000 cases in all of sub-Saharan Africa) have happened since 2009.

Note:
Link to Learning

This [movie](#) discusses the pathogenesis of *Trypanosoma brucei*, the causative agent of African sleeping sickness.

In Latin America, another species, *T. cruzi*, is responsible for Chagas disease. *T. cruzi* infections are mainly caused by a blood-sucking bug. The parasite inhabits heart and digestive system tissues in the chronic phase of infection, leading to malnutrition and heart failure due to abnormal heart rhythms. An estimated 10 million people are infected with Chagas disease, and it caused 10,000 deaths in 2008.
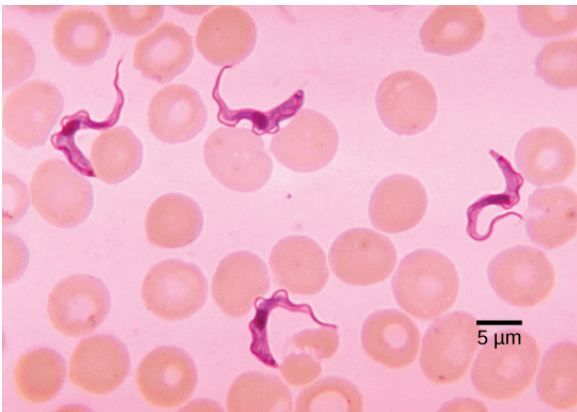
Trypanosomes are shown among red blood cells. (credit: modification of work by Dr. Myron G. Shultz; scale-bar data from Matt Russell)

Plant Parasites

Protist parasites of terrestrial plants include agents that destroy food crops. The oomycete *Plasmopara viticola* parasitizes grape plants, causing a disease called downy mildew ([link]). Grape plants infected with *P. viticola* appear stunted and have discolored, withered leaves. The spread of downy mildew nearly collapsed the French wine industry in the nineteenth century.
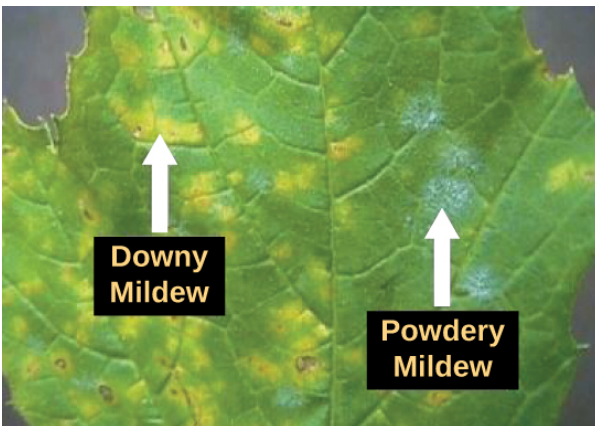
Both downy and powdery mildews on this grape leaf are caused by an infection of *P. viticola*. (credit: modification of work by USDA)

Phytophthora infestans is an oomycete responsible for potato late blight, which causes potato stalks and stems to decay into black slime ([link]). Widespread potato blight caused by *P. infestans* precipitated the well-known Irish potato famine in the nineteenth century that claimed the lives of approximately 1 million people and led to the emigration of at least 1 million more from Ireland. Late blight continues to plague potato crops in certain parts of the United States and Russia, wiping out as much as 70 percent of crops when no pesticides are applied.

These unappetizing remnants result from an infection with *P. infestans*, the causative agent of potato late blight. (credit: USDA)

Agents of Decomposition

The fungus-like protist saprobes are specialized to absorb nutrients from nonliving organic matter, such as dead organisms or their wastes. For instance, many types of oomycetes grow on dead animals or algae. Saprobic protists have the essential function of returning inorganic nutrients to the soil and water. This process allows for new plant growth, which in turn generates sustenance for other organisms along the food chain. Indeed, without saprobe species, such as protists, fungi, and bacteria, life would cease to exist as all organic carbon became "tied up" in dead organisms.

Section Summary

Protists function at several levels of the ecological food web: as primary producers, as direct food sources, and as decomposers. In addition, many protists are parasites of plants and animals that can cause deadly human diseases or destroy valuable crops.

Review Questions

Exercise:

Problem: An example of carbon fixation is _____.

    a. photosynthesis
    b. decomposition
    c. phagocytosis
    d. parasitism

Solution:

A

Exercise:

Problem:

Which parasitic protist evades the host immune system by altering its surface proteins with each generation?

    a. *Paramecium caudatum*
    b. *Trypanosoma brucei*
    c. *Plasmodium falciparum*
    d. *Phytophthora infestans*

Solution:

B

Free Response

Exercise:

Problem:

How does killing *Anopheles* mosquitoes affect the *Plasmodium* protists?

Solution:

Plasmodium parasites infect humans and cause malaria. However, they must complete part of their life cycle within *Anopheles* mosquitoes, and they can only infect humans via the bite wound of a mosquito. If the mosquito population is decreased, then fewer *Plasmodium* would be able to develop and infect humans, thereby reducing the incidence of human infections with this parasite.

Exercise:

Problem:

Without treatment, why does African sleeping sickness invariably lead to death?

Solution:

The trypanosomes that cause this disease are capable of expressing a glycoprotein coat with a different molecular structure with each generation. Because the immune system must respond to specific antigens to raise a meaningful defense, the changing nature of trypanosome antigens prevents the immune system from ever clearing this infection. Massive trypanosome infection eventually leads to host organ failure and death.

Introduction
class="introduction"

Many species of fungus produce the familiar mushroom (a) which is a reproductive structure. This (b) coral fungus displays brightly colored fruiting bodies. This electron micrograph shows (c) the spore-bearing structures of *Aspergillus*, a type of toxic fungi found mostly in soil and plants. (credit "mushroom": modification of work by Chris Wee; credit "coral fungus": modification of work by

(a)   (b)   (c)
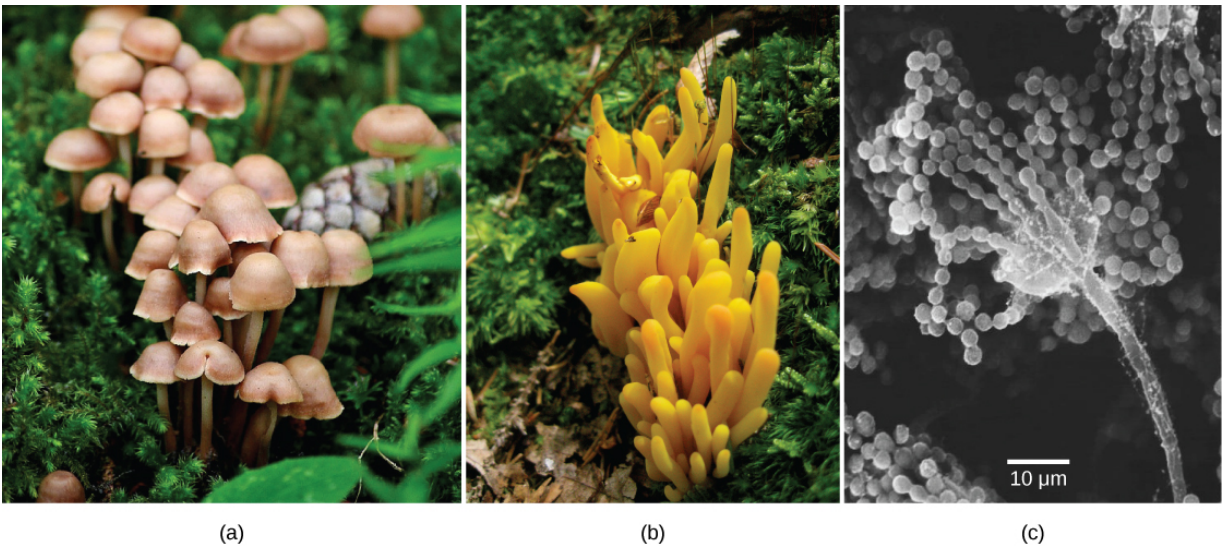
The word *fungus* comes from the Latin word for mushrooms. Indeed, the familiar mushroom is a reproductive structure used by many types of fungi. However, there are also many fungi species that don't produce mushrooms at all. Being eukaryotes, a typical fungal cell contains a true nucleus and many membrane-bound organelles. The kingdom Fungi includes an enormous variety of living organisms collectively referred to as Eucomycota, or true Fungi. While scientists have identified about 100,000 species of fungi, this is only a fraction of the 1.5 million species of fungus likely present on Earth. Edible mushrooms, yeasts, black mold, and the producer of the antibiotic penicillin, *Penicillium notatum*, are all members of the kingdom Fungi, which belongs to the domain Eukarya.

Fungi, once considered plant-like organisms, are more closely related to animals than plants. Fungi are not capable of photosynthesis: they are heterotrophic because they use complex organic compounds as sources of energy and carbon. Some fungal organisms multiply only asexually, whereas others undergo both asexual reproduction and sexual reproduction with alternation of generations. Most fungi produce a large number of **spores**, which are haploid cells that can undergo mitosis to form multicellular, haploid individuals. Like bacteria, fungi play an essential role in ecosystems because they are decomposers and participate in the cycling of nutrients by breaking down organic materials to simple molecules.

Fungi often interact with other organisms, forming beneficial or mutualistic associations. For example most terrestrial plants form symbiotic relationships with fungi. The roots of the plant connect with the underground parts of the fungus forming **mycorrhizae**. Through mycorrhizae, the fungus and plant exchange nutrients and water, greatly aiding the survival of both species Alternatively, lichens are an association between a fungus and its photosynthetic partner (usually an alga). Fungi also cause serious infections in plants and animals. For example, Dutch elm disease, which is caused by the fungus *Ophiostoma ulmi,* is a particularly devastating type of fungal infestation that destroys many native species of elm (*Ulmus* sp.) by infecting the tree's vascular system. The elm bark beetle acts as a vector, transmitting the disease from tree to tree. Accidentally introduced in the 1900s, the fungus decimated elm trees across the continent. Many European and Asiatic elms are less susceptible to Dutch elm disease than American elms.

In humans, fungal infections are generally considered challenging to treat. Unlike bacteria, fungi do not respond to traditional antibiotic therapy, since they are eukaryotes. Fungal infections may prove deadly for individuals with compromised immune systems.

Fungi have many commercial applications. The food industry uses yeasts in baking, brewing, and cheese and wine making. Many industrial compounds are byproducts of fungal fermentation. Fungi are the source of many commercial enzymes and antibiotics.

Glossary

spore
>   a haploid cell that can undergo mitosis to form a multicellular, haploid
>   individua

mycorrhizae
>   a mutualistic relationship between a plant and a fungus. Mycorrhizae
>   are connections between fungal hyphae, which provide soil minerals to
>   the plant, and plant roots, which provide carbohydrates to the fungus

Characteristics of Fungi
By the end of this section, you will be able to:

- List the characteristics of fungi
- Describe the composition of the mycelium
- Describe the mode of nutrition of fungi
- Explain sexual and asexual reproduction in fungi

Although humans have used yeasts and mushrooms since prehistoric times, until recently, the biology of fungi was poorly understood. Up until the mid-20th century, many scientists classified fungi as plants. Fungi, like plants, arose mostly sessile and seemingly rooted in place. They possess a stem-like structure similar to plants, as well as having a root-like fungal mycelium in the soil. In addition, their mode of nutrition was poorly understood. Progress in the field of fungal biology was the result of **mycology**: the scientific study of fungi. Based on fossil evidence, fungi appeared in the pre-Cambrian era, about 450 million years ago. Molecular biology analysis of the fungal genome demonstrates that fungi are more closely related to animals than plants. They are a polyphyletic group of organisms that share characteristics, rather than sharing a single common ancestor.

Note:
Career Connection
Mycologist
Mycologists are biologists who study fungi. Mycology is a branch of microbiology, and many mycologists start their careers with a degree in microbiology. To become a mycologist, a bachelor's degree in a biological science (preferably majoring in microbiology) and a master's degree in mycology are minimally necessary. Mycologists can specialize in taxonomy and fungal genomics, molecular and cellular biology, plant pathology, biotechnology, or biochemistry. Some medical microbiologists concentrate on the study of infectious diseases caused by fungi (mycoses). Mycologists collaborate with zoologists and plant pathologists to identify and control difficult fungal infections, such as the devastating chestnut blight, the mysterious decline in frog populations in many areas of the

world, or the deadly epidemic called white nose syndrome, which is decimating bats in the Eastern United States.

Government agencies hire mycologists as research scientists and technicians to monitor the health of crops, national parks, and national forests. Mycologists are also employed in the private sector by companies that develop chemical and biological control products or new agricultural products, and by companies that provide disease control services. Because of the key role played by fungi in the fermentation of alcohol and the preparation of many important foods, scientists with a good understanding of fungal physiology routinely work in the food technology industry. Oenology, the science of wine making, relies not only on the knowledge of grape varietals and soil composition, but also on a solid understanding of the characteristics of the wild yeasts that thrive in different wine-making regions. It is possible to purchase yeast strains isolated from specific grape-growing regions. The great French chemist and microbiologist, Louis Pasteur, made many of his essential discoveries working on the humble brewer's yeast, thus discovering the process of fermentation.

Cell Structure and Function

Fungi are eukaryotes, and as such, have a complex cellular organization. As eukaryotes, fungal cells contain a membrane-bound nucleus. The DNA in the nucleus is wrapped around histone proteins, as is observed in other eukaryotic cells. A few types of fungi have structures comparable to bacterial plasmids (loops of DNA); however, the horizontal transfer of genetic information from one mature bacterium to another rarely occurs in fungi. Fungal cells also contain mitochondria and a complex system of internal membranes, including the endoplasmic reticulum and Golgi apparatus.

Unlike plant cells, fungal cells do not have chloroplasts or chlorophyll. Many fungi display bright colors arising from other cellular pigments, ranging from red to green to black. The poisonous *Amanita muscaria* (fly agaric) is recognizable by its bright red cap with white patches ([link]).

Pigments in fungi are associated with the cell wall and play a protective role against ultraviolet radiation. Some fungal pigments are toxic.

The poisonous *Amanita muscaria* is native to temperate and boreal regions of North America. (credit: Christine Majul)

Like plant cells, fungal cells have a thick cell wall. The rigid layers of fungal cell walls contain complex polysaccharides called chitin and glucans. Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The wall protects the cell from desiccation and predators. Fungi have plasma membranes similar to other eukaryotes, except that the structure is stabilized by ergosterol: a steroid molecule that replaces the cholesterol found in animal cell membranes. Most members of the kingdom Fungi are nonmotile. Flagella are produced only by the gametes in the primitive Phylum Chytridiomycota.

Growth

The vegetative body of a fungus is a unicellular or multicellular **thallus**. Dimorphic fungi can change from the unicellular to multicellular state depending on environmental conditions. Unicellular fungi are generally referred to as **yeasts**. *Saccharomyces cerevisiae* (baker's yeast) and *Candida* species (the agents of thrush, a common fungal infection) are examples of unicellular fungi ([link]).
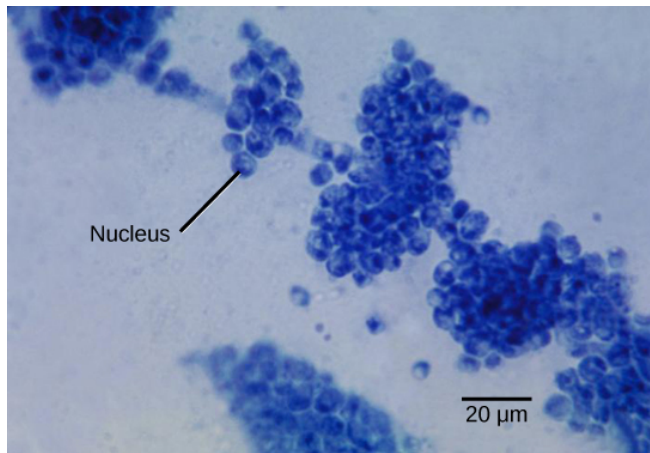
Candida albicans is a yeast cell and the agent of candidiasis and thrush. This organism has a similar morphology to coccus bacteria; however, yeast is a eukaryotic organism (note the nucleus). (credit: modification of work by Dr. Godon Roberstad, CDC; scale-bar data from Matt Russell)

Most fungi are multicellular organisms. They display two distinct morphological stages: the vegetative and reproductive. The vegetative stage consists of a tangle of slender thread-like structures called **hyphae** (singular, **hypha**), whereas the reproductive stage can be more conspicuous. The mass of hyphae is a **mycelium** ([link]). It can grow on a surface, in soil or decaying material, in a liquid, or even on living tissue. Although

individual hyphae must be observed under a microscope, the mycelium of a fungus can be very large, with some species truly being "the fungus humongous." The giant *Armillaria solidipes* (honey mushroom) is considered the largest organism on Earth, spreading across more than 2,000 acres of underground soil in eastern Oregon; it is estimated to be at least 2,400 years old.
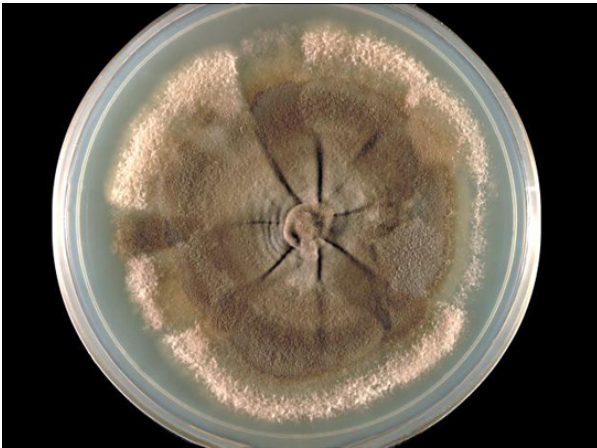
The mycelium of the fungus *Neotestudina rosati* can be pathogenic to humans. The fungus enters through a cut or scrape and develops a mycetoma, a chronic subcutaneous infection. (credit: CDC)

Most fungal hyphae are divided into separate cells by endwalls called **septa** (singular, **septum**) ([link]**a, c**). In most phyla of fungi, tiny holes in the septa allow for the rapid flow of nutrients and small molecules from cell to cell along the hypha. They are described as perforated septa. The hyphae in bread molds (which belong to the Phylum Zygomycota) are not separated by septa. Instead, they are formed by large cells containing many nuclei, an arrangement described as **coenocytic hyphae** ([link]**b**).
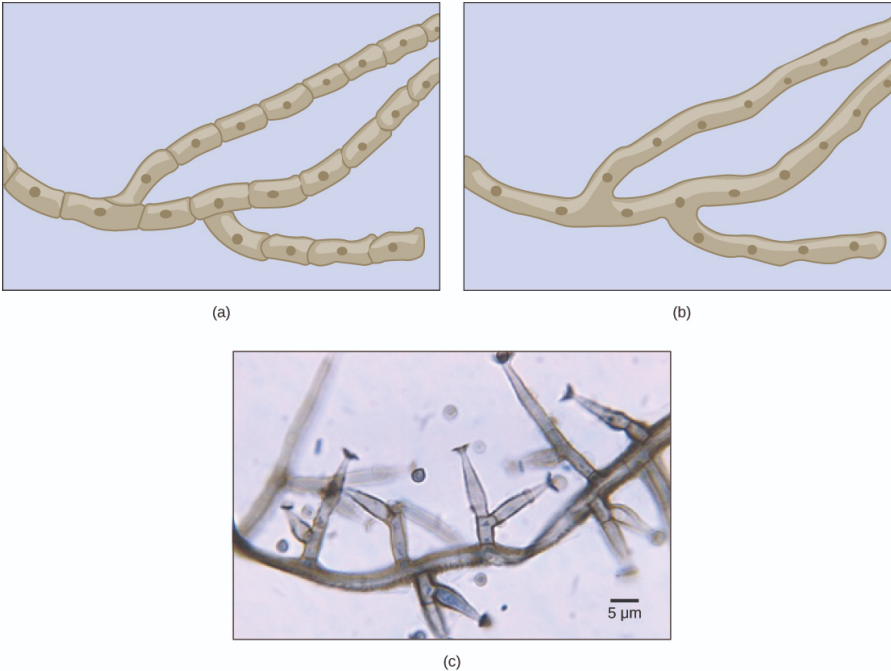
Fungal hyphae may be (a) septated or (b) coenocytic (coeno- = "common"; -cytic = "cell") with many nuclei present in a single hypha. A bright field light micrograph of (c) *Phialophora richardsiae* shows septa that divide the hyphae. (credit c: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Fungi thrive in environments that are moist and slightly acidic, and can grow with or without light. They vary in their oxygen requirement. Most fungi are **obligate aerobes**, requiring oxygen to survive. Other species, such as the Chytridiomycota that reside in the rumen of cattle, are are **obligate anaerobes**, in that they only use anaerobic respiration because oxygen will disrupt their metabolism or kill them. Yeasts are intermediate, being **faculative anaerobes**. This means that they grow best in the presence of oxygen using aerobic respiration, but can survive using anaerobic respiration when oxygen is not available. The alcohol produced from yeast fermentation is used in wine and beer production.

Nutrition

Like animals, fungi are heterotrophs; they use complex organic compounds as a source of carbon, rather than fix carbon dioxide from the atmosphere as do some bacteria and most plants. In addition, fungi do not fix nitrogen from the atmosphere. Like animals, they must obtain it from their diet. However, unlike most animals, which ingest food and then digest it internally in specialized organs, fungi perform these steps in the reverse order; digestion precedes ingestion. First, exoenzymes are transported out of the hyphae, where they process nutrients in the environment. Then, the smaller molecules produced by this external digestion are absorbed through the large surface area of the mycelium. As with animal cells, the polysaccharide of storage is glycogen, rather than starch, as found in plants.

Fungi are mostly **saprobes** (saprophyte is an equivalent term): organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter: mainly plant material. Fungal exoenzymes are able to break down insoluble polysaccharides, such as the cellulose and lignin of dead wood, into readily absorbable glucose molecules. The carbon, nitrogen, and other elements are thus released into the environment. Because of their varied metabolic pathways, fungi fulfill an important ecological role and are being investigated as potential tools in bioremediation. For example, some species of fungi can be used to break down diesel oil and polycyclic aromatic hydrocarbons (PAHs). Other species take up heavy metals, such as cadmium and lead.

Some fungi are parasitic, infecting either plants or animals. Smut and Dutch elm disease affect plants, whereas athlete's foot and candidiasis (thrush) are medically important fungal infections in humans. In environments poor in nitrogen, some fungi resort to predation of nematodes (small non-segmented roundworms). Species of *Arthrobotrys* fungi have a number of mechanisms to trap nematodes. One mechanism involves constricting rings within the network of hyphae. The rings swell when they touch the nematode, gripping it in a tight hold. The fungus penetrates the tissue of the worm by extending specialized hyphae called **haustoria**. Many parasitic fungi possess haustoria, as these structures penetrate the tissues of the host,

release digestive enzymes within the host's body, and absorb the digested nutrients.

Reproduction

Fungi reproduce sexually and/or asexually. Perfect fungi reproduce both sexually and asexually, while the so-called imperfect fungi reproduce only asexually (by mitosis).

In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by either floating on the wind or hitching a ride on an animal. Fungal spores are smaller and lighter than plant seeds. The giant puffball mushroom bursts open and releases trillions of spores. The huge number of spores released increases the likelihood of landing in an environment that will support growth ([link]).

(a)   (b)

The (a) giant puff ball mushroom releases (b) a cloud of spores when it reaches maturity. (credit a: modification of work by Roger Griffith; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

Asexual Reproduction

Fungi reproduce asexually by fragmentation, budding, or producing spores. Fragments of hyphae can grow new colonies. Somatic cells in yeast form buds. During budding (a type of cytokinesis), a bulge forms on the side of the cell, the nucleus divides mitotically, and the bud ultimately detaches itself from the mother cell ([link]).
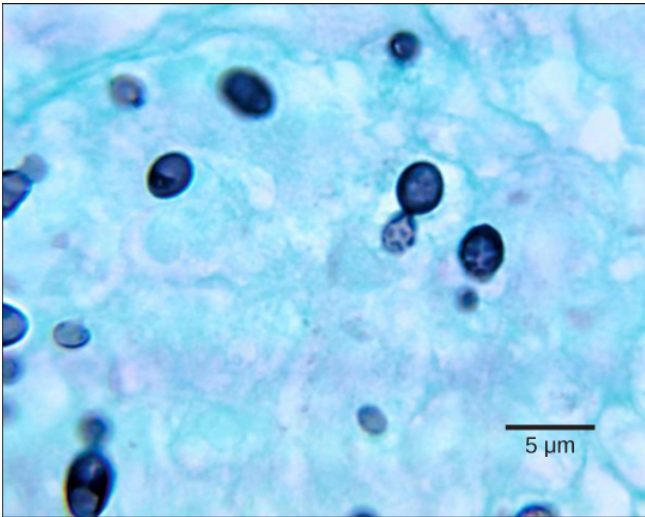
The dark cells in this bright field light micrograph are the pathogenic yeast *Histoplasma capsulatum*, seen against a backdrop of light blue tissue. Histoplasma primarily infects lungs but can spread to other tissues, causing histoplasmosis, a potentially fatal disease. (credit: modification of work by Dr. Libero Ajello, CDC; scale-bar data from Matt Russell)

The most common mode of asexual reproduction is through the formation of asexual spores, which are produced by one parent only (through mitosis) and are genetically identical to that parent ([link]). Spores allow fungi to expand their distribution and colonize new environments. They may be released from the parent thallus either outside or within a special reproductive sac called a **sporangium**.
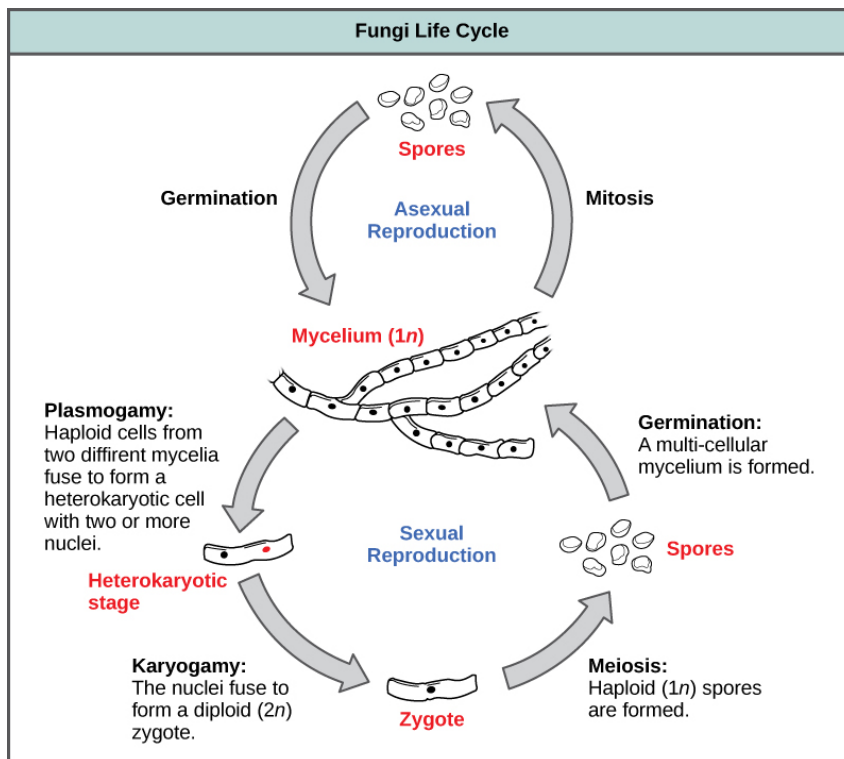
Fungi may have both asexual and sexual stages of reproduction.

There are many types of asexual spores. Conidiospores are unicellular or multicellular spores that are released directly from the tip or side of the hypha. Other asexual spores originate in the fragmentation of a hypha to form single cells that are released as spores; some of these have a thick wall surrounding the fragment. Yet others bud off the vegetative parent cell. Sporangiospores are produced in a sporangium ([link]).
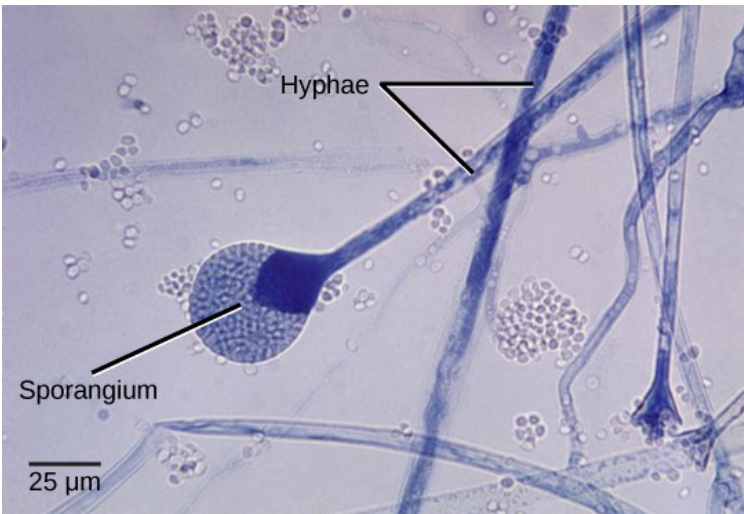
This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a *Mucor* sp. fungus, a mold often found indoors. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Sexual Reproduction

Sexual reproduction introduces genetic variation into a population of fungi. In fungi, sexual reproduction often occurs in response to adverse environmental conditions. During sexual reproduction, two mating types are produced. When both mating types are present in the same mycelium, it is called **homothallic**, or self-fertile. **Heterothallic** mycelia require two different, but compatible, mycelia to reproduce sexually.

Although there are many variations in fungal sexual reproduction, all include the following three stages ([link]). First, during **plasmogamy** (literally, "marriage or union of cytoplasm"), two haploid cells fuse, leading

to a dikaryotic stage where two haploid nuclei coexist in a single cell. During **karyogamy** ("nuclear marriage"), the haploid nuclei fuse to form a diploid zygote nucleus. Finally, meiosis takes place in the gametangia (singular, gametangium) organs, in which gametes of different mating types are generated. At this stage, spores are disseminated into the environment.

Section Summary

Fungi are eukaryotic organisms that appeared on land more than 450 million years ago. They are heterotrophs and contain neither photosynthetic pigments such as chlorophyll, nor organelles such as chloroplasts. Because fungi feed on decaying and dead matter, they are saprobes. Fungi are important decomposers that release essential elements into the environment. External enzymes digest nutrients that are absorbed by the body of the fungus, which is called a thallus. A thick cell wall made of chitin surrounds the cell. Fungi can be unicellular as yeasts, or develop a network of filaments called a mycelium, which is often described as mold. Most species multiply by asexual and sexual reproductive cycles and display an alternation of generations. Another group of fungi do not have a sexual cycle. Sexual reproduction involves plasmogamy (the fusion of the

cytoplasm), followed by karyogamy (the fusion of nuclei). Meiosis regenerates haploid individuals, resulting in haploid spores.

Review Questions

Exercise:

Problem:

Which polysaccharide is usually found in the cell wall of fungi?

  a. starch
  b. glycogen
  c. chitin
  d. cellulose

Solution:

C

Exercise:

Problem: Which of these organelles is not found in a fungal cell?

  a. chloroplast
  b. nucleus
  c. mitochondrion
  d. Golgi apparatus

Solution:

A

Exercise:

Problem:

The wall dividing individual cells in a fungal filament is called a

a. thallus
b. hypha
c. mycelium
d. septum

Solution:

D

Exercise:

Problem:

During sexual reproduction, a homothallic mycelium contains

a. all septated hyphae
b. all haploid nuclei
c. both mating types
d. none of the above

Solution:

C

Free Response

Exercise:

Problem:

What are the evolutionary advantages for an organism to reproduce both asexually and sexually?

Solution:

Asexual reproduction is fast and best under favorable conditions. Sexual reproduction allows the recombination of genetic traits and

increases the odds of developing new adaptations better suited to a changed environment.

Exercise:

Problem:

Compare plants, animals, and fungi, considering these components: cell wall, chloroplasts, plasma membrane, food source, and polysaccharide storage. Be sure to indicate fungi's similarities and differences to plants and animals.

Solution:

Animals have no cell walls; fungi have cell walls containing chitin; plants have cell walls containing cellulose. Chloroplasts are absent in both animals and fungi but are present in plants. Animal plasma membranes are stabilized with cholesterol, while fungi plasma membranes are stabilized with ergosterol, and plant plasma membranes are stabilized with phytosterols. Animals obtain N and C from food sources via internal digestion. Fungi obtain N and C from food sources via external digestion. Plants obtain organic N from the environment or through symbiotic N-fixing bacteria; they obtain C from photosynthesis. Animals and fungi store polysaccharides as glycogen, while plants store them as starch.

Glossary

coenocytic hypha
> single hypha that lacks septa and contains many nuclei

faculative anaerobes
> organisms that can perform both aerobic and anaerobic respiration and can survive in oxygen-rich and oxygen-poor environment

haustoria
> modified hyphae on many parasitic fungi that penetrate the tissues of their hosts, release digestive enzymes, and/or absorb nutrients from the

host

heterothallic
describes when only one mating type is present in an individual mycelium

homothallic
describes when both mating types are present in mycelium

hypha
fungal filament composed of one or more cells

karyogamy
fusion of nuclei

mycelium
mass of fungal hyphae

mycology
scientific study of fungi

obligate aerobes
organisms, such as humans, that must perform aerobic respiration to survive

obligate anaerobes
organisms that only perform anaerobic respiration and often cannot survive in the presence of oxygen

plasmogamy
fusion of cytoplasm

saprobe
organism that derives nutrients from decaying organic matter; also saprophyte

septa
cell wall division between hyphae

sporangium
    reproductive sac that contains spores

thallus
    vegetative body of a fungus

yeast
    general term used to describe unicellular fungi

Classifications of Fungi
By the end of this section, you will be able to:

- Classify fungi into the five major phyla
- Describe each phylum in terms of major representative species and patterns of reproduction

The kingdom Fungi contains five major phyla that were established according to their mode of sexual reproduction or using molecular data. Polyphyletic, unrelated fungi that reproduce without a sexual cycle, are placed for convenience in a sixth group called a "form phylum". Not all mycologists agree with this scheme. Rapid advances in molecular biology and the sequencing of 18S rRNA (a part of RNA) continue to show new and different relationships between the various categories of fungi.

The five true phyla of fungi are the Chytridiomycota (Chytrids), the Zygomycota (conjugated fungi), the Ascomycota (sac fungi), the Basidiomycota (club fungi) and the recently described Phylum Glomeromycota. An older classification scheme grouped fungi that strictly use asexual reproduction into Deuteromycota, a group that is no longer in use.

Note: "-mycota" is used to designate a phylum while "-mycetes" formally denotes a class or is used informally to refer to all members of the phylum.

Chytridiomycota: The Chytrids

The only class in the Phylum Chytridiomycota is the **Chytridiomycetes**. The chytrids are the simplest and most primitive Eumycota, or true fungi. The evolutionary record shows that the first recognizable chytrids appeared during the late pre-Cambrian period, more than 500 million years ago. Like all fungi, chytrids have chitin in their cell walls, but one group of chytrids has both cellulose and chitin in the cell wall. Most chytrids are unicellular; a few form multicellular organisms and hyphae, which have no septa between cells (coenocytic). They produce gametes and diploid zoospores that swim with the help of a single flagellum.

The ecological habitat and cell structure of chytrids have much in common with protists. Chytrids usually live in aquatic environments, although some species live on land. Some species thrive as parasites on plants, insects, or amphibians ([link]), while others are saprobes. The chytrid species *Allomyces* is well characterized as an experimental organism. Its reproductive cycle includes both asexual and sexual phases. *Allomyces* produces diploid or haploid flagellated zoospores in a sporangium.
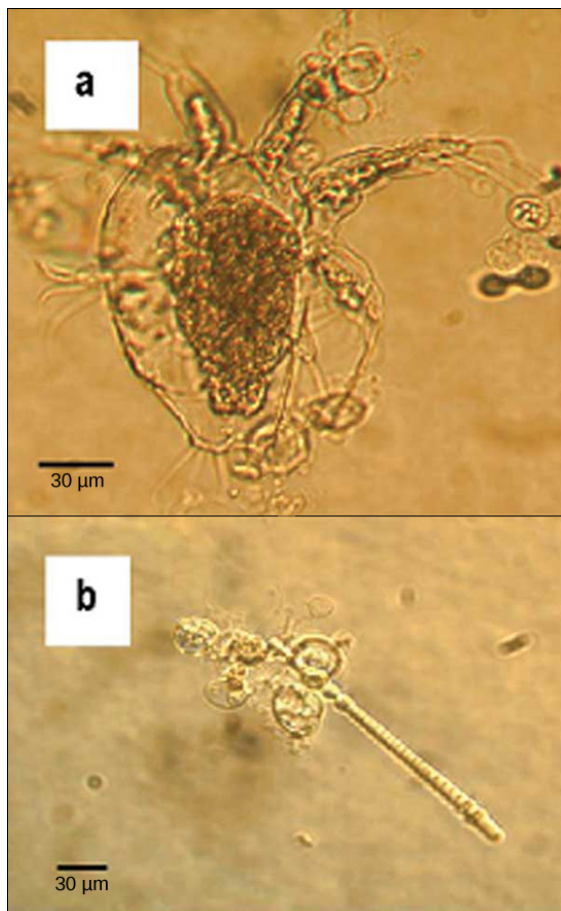
The chytrid *Batrachochytrium dendrobatidis* is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod and (b) algae. This chytrid

causes skin diseases in many
species of amphibians,
resulting in species decline
and extinction. (credit:
modification of work by
Johnson ML, Speare R.,
CDC)

Zygomycota: The Conjugated Fungi

The zygomycetes are a relatively small group of fungi belonging to the Phylum **Zygomycota**. They include the familiar bread mold, *Rhizopus stolonifer*, which rapidly propagates on the surfaces of breads, fruits, and vegetables. Most species are saprobes, living off decaying organic material; a few are parasites, particularly of insects. Zygomycetes play a considerable commercial role. The metabolic products of other species of *Rhizopus* are intermediates in the synthesis of semi-synthetic steroid hormones.

Zygomycetes have a thallus of coenocytic hyphae in which the nuclei are haploid when the organism is in the vegetative stage. The fungi usually reproduce asexually by producing sporangiospores ([link]). The black tips of bread mold are the swollen sporangia packed with black spores ([link]). When spores land on a suitable substrate, they germinate and produce a new mycelium. Sexual reproduction starts when conditions become unfavorable. Two opposing mating strains (type + and type –) must be in close proximity for gametangia from the hyphae to be produced and fuse, leading to karyogamy. The developing diploid **zygospores** have thick coats that protect them from desiccation and other hazards. They may remain dormant until environmental conditions are favorable. When the zygospore germinates, it undergoes meiosis and produces haploid spores, which will, in turn, grow into a new organism. This form of sexual reproduction in fungi is called conjugation (although it differs markedly from conjugation in bacteria and protists), giving rise to the name "conjugated fungi".

Zygomycete Life Cycle

Mycelia

Germination

Asexual reproduction

Mitosis

Germination:
Mycelia form. If the two mating types (+ and –) are in close proximity, extensions called gametangia form between them.

Spores

Germination

+ Mating type

Gametangia

Mycelia (1n)

Sporangium (1n)

– Mating type

Sexual reproduction

Plasmogamy:
Fusion between + and – mating types results in a zygosporangium with multiple haploid nuclei. The zygosporangium forms a thick, protective coat.

Meiosis and germination:
A sporangium grows on a short stalk. Haploid spores are formed inside.

Zygosporangium

Karyogamy:
The nuclei fuse to form a zygote with multiple diploid nuclei.

Zygote (2n)

Zygomycetes have asexual and asexual life cycles. In the sexual life cycle, plus and minus mating types conjugate to form a zygosporangium.

Sporangia grow at the end of stalks, which appear as (a) white fuzz seen on this bread mold, *Rhizopus stolonifer*. The (b) tips of bread mold are the spore-containing sporangia. (credit b: modification of work by "polandeze"/Flickr)

Ascomycota: The Sac Fungi

The majority of known fungi belong to the Phylum **Ascomycota**, which is characterized by the formation of an **ascus** (plural, asci), a sac-like structure that contains haploid ascospores. Many ascomycetes are of commercial importance. Some play a beneficial role, such as the yeasts used in baking, brewing, and wine fermentation, plus truffles and morels, which are held as gourmet delicacies. *Aspergillus oryzae* is used in the fermentation of rice to produce sake. Other ascomycetes parasitize plants and animals, including humans. For example, fungal pneumonia poses a significant threat to AIDS patients who have a compromised immune system. Ascomycetes not only infest and destroy crops directly; they also produce poisonous secondary metabolites that make crops unfit for consumption. Filamentous ascomycetes produce hyphae divided by perforated septa, allowing streaming of cytoplasm from one cell to the other. Conidia and asci, which are used respectively for asexual and sexual reproductions, are usually separated from the vegetative hyphae by blocked (non-perforated) septa.

Asexual reproduction is frequent and involves the production of conidiophores that release haploid conidiospores ([link]). Sexual

reproduction starts with the development of special hyphae from either one of two types of mating strains ([link]). The "male" strain produces an antheridium and the "female" strain develops an ascogonium. At fertilization, the antheridium and the ascogonium combine in plasmogamy without nuclear fusion. Special ascogenous hyphae arise, in which pairs of nuclei migrate: one from the "male" strain and one from the "female" strain. In each ascus, two or more haploid ascospores fuse their nuclei in karyogamy. During sexual reproduction, thousands of asci fill a fruiting body called the **ascocarp**. The diploid nucleus gives rise to haploid nuclei by meiosis. The ascospores are then released, germinate, and form hyphae that are disseminated in the environment and start new mycelia ([link]).

Note:
Art Connection

Ascomycete Life Cycle

Spores

Mitosis

Germination

Asexual Reproduction

Plasmogamy and mitosis: The ascogonium and antheridium fuse. Mitosis and cell division result in the formation of many dikaryotic hyphae, which form a fruiting body called the ascocarp. Asci form at the tips of these hyphae.

Conidiophore

Mycelia

Dispersal and germination

Ascogonium **Antheridium**

Ascospores (1n)

Ascus

Sexual Reproduction

Mitosis and cell division: Eight haploid ascospores are formed.

Ascocarp

Karyogamy: The nuclei in the asci fuse to form a diploid zygote.

Zygote (2n)

Meiosis: An ascus with four haploid nuclei is formed.

The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle.

Which of the following statements is true?

a. A dikaryotic ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.

b. A diploid ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.

c. A haploid zygote that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.

d. A dikaryotic ascus that forms in the ascocarp undergoes plasmogamy, meiosis, and mitosis to form eight ascospores.
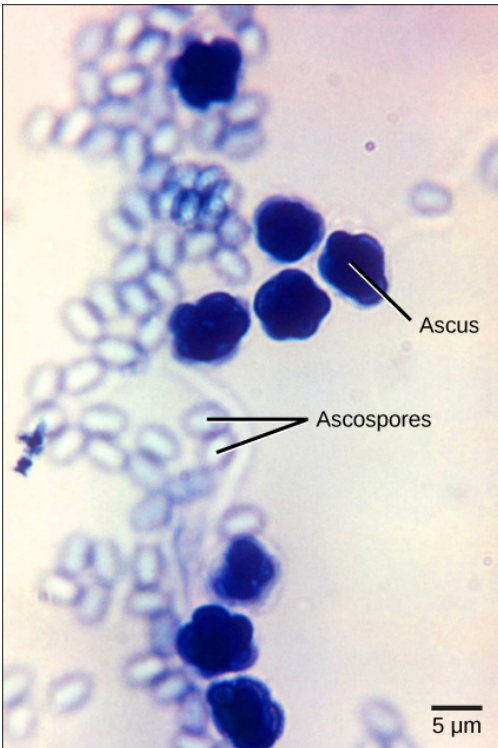
The bright field light micrograph shows ascospores being released from asci in the fungus *Talaromyces flavus* var. *flavus*. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Basidiomycota: The Club Fungi

The fungi in the Phylum **Basidiomycota** are easily recognizable under a light microscope by their club-shaped fruiting bodies called **basidia** (singular, **basidium**), which are the swollen terminal cell of a hypha. The basidia, which are the reproductive organs of these fungi, are often contained within the familiar mushroom, commonly seen in fields after rain, on the supermarket shelves, and growing on your lawn ([link]). These mushroom-producing basidiomyces are sometimes referred to as "gill fungi" because of the presence of gill-like structures on the underside of the cap. The "gills" are actually compacted hyphae on which the basidia are borne. This group also includes shelf fungus, which cling to the bark of trees like small shelves. In addition, the basidiomycota includes smuts and rusts, which are important plant pathogens; toadstools, and shelf fungi stacked on tree trunks. Most edible fungi belong to the Phylum Basidiomycota; however, some basidiomycetes produce deadly toxins. For example, *Cryptococcus neoformans* causes severe respiratory illness.

The fruiting bodies of a basidiomycete form a ring in a meadow, commonly called "fairy ring." The best-known fairy ring fungus has the scientific name *Marasmius oreades*. The body of this

fungus, its mycelium, is underground and grows outward in a circle. As it grows, the mycelium depletes the soil of nitrogen, causing the mycelia to grow away from the center and leading to the "fairy ring" of fruiting bodies where there is adequate soil nitrogen. (Credit: "Cropcircles"/Wikipedia Commons)]

The lifecycle of basidiomycetes includes alternation of generations ([link]). Spores are generally produced through sexual reproduction, rather than asexual reproduction. The club-shaped basidium carries spores called basidiospores. In the basidium, nuclei of two different mating strains fuse (karyogamy), giving rise to a diploid zygote that then undergoes meiosis. The haploid nuclei migrate into basidiospores, which germinate and generate monokaryotic hyphae. The mycelium that results is called a primary mycelium. Mycelia of different mating strains can combine and produce a secondary mycelium that contains haploid nuclei of two different mating strains. This is the dikaryotic stage of the basidiomyces lifecyle and and it is the dominant stage. Eventually, the secondary mycelium generates a **basidiocarp**, which is a fruiting body that protrudes from the ground— this is what we think of as a mushroom. The basidiocarp bears the developing basidia on the gills under its cap.

Note:
Art Connection

Basidiomycete Life Cycle

Basidiospores (n)

Germination:
Mycelia form. There are two mating types (+ and –).

+ Mating type

Mycelia (1n)

– Mating type

Dispersal and germination

Plasmogamy:
Fusion between + and – mating types results in formation of a dikaryotic mycelium.

Sexual Reproduction

Cell division:
Four basidiospores are formed.

Basidium with four nuclei (1n)

Meiosis:
Four haploid nuclei are formed in the basidium.

Mitosis:
Under the right environmental conditions, a basidiocarp forms. Gills of the basidiocarp contain cells called basidia.

Zygote (2n)

Basidia

Karyogamy:
Basidia form diploid nuclei.

Basidiocarp

The lifecycle of a basidiomycete alternates generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae.

Which of the following statements is true?

a. A basidium is the fruiting body of a mushroom-producing fungus, and it forms four basidiocarps.
b. The result of the plasmogamy step is four basidiospores.
c. Karyogamy results directly in the formation of mycelia.
d. A basidiocarp is the fruiting body of a mushroom-producing fungus.

Asexual Ascomycota and Basidiomycota

Imperfect fungi—those that do not display a sexual phase—use to be classified in the form phylum **Deuteromycota**, , a classification group no longer used in the present, ever-developing classification of organisms. While Deuteromycota use to be a classification group, recent moleclular analysis has shown that the members classified in this group belong to the Ascomycota or the Basidiomycota classifications. Since they do not possess the sexual structures that are used to classify other fungi, they are less well described in comparison to other members. Most members live on land, with a few aquatic exceptions. They form visible mycelia with a fuzzy appearance and are commonly known as **mold**.

Reproduction of the fungi in this group is strictly asexual and occurs mostly by production of asexual conidiospores ([link]). Some hyphae may recombine and form heterokaryotic hyphae. Genetic recombination is known to take place between the different nuclei.
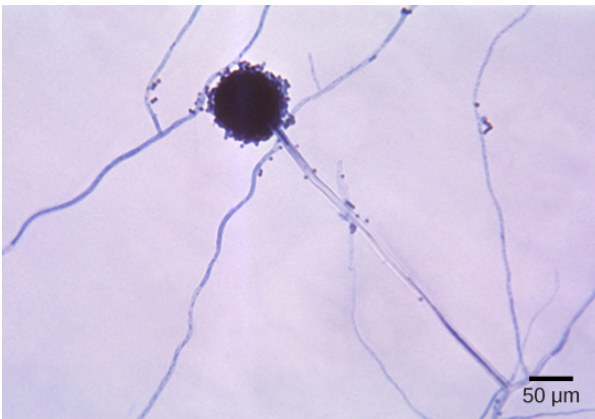
Aspergillus niger is an asexually reproducing fungus (phylum Ascomycota) commonly found as a food contaminant. The spherical structure in this light micrograph is a conidiophore.

The fungi in this group have a large impact on everyday human life. The food industry relies on them for ripening some cheeses. The blue veins in Roquefort cheese and the white crust on Camembert are the result of fungal growth. The antibiotic penicillin was originally discovered on an overgrown Petri plate, on which a colony of *Penicillium* fungi killed the bacterial growth surrounding it. Other fungi in this group cause serious diseases, either directly as parasites (which infect both plants and humans), or as producers of potent toxic compounds, as seen in the aflatoxins released by fungi of the genus *Aspergillus*.

Glomeromycota

The **Glomeromycota** is a newly established phylum which comprises about 230 species that all live in close association with the roots of trees. Fossil records indicate that trees and their root symbionts share a long evolutionary history. It appears that all members of this family form **arbuscular mycorrhizae**: the hyphae interact with the root cells forming a mutually beneficial association where the plants supply the carbon source and energy in the form of carbohydrates to the fungus, and the fungus supplies essential minerals from the soil to the plant.

The glomeromycetes do not reproduce sexually and do not survive without the presence of plant roots. Although they have coenocytic hyphae like the zygomycetes, they do not form zygospores. DNA analysis shows that all glomeromycetes probably descended from a common ancestor, making them a monophyletic lineage.

Section Summary

Chytridiomycota (chytrids) are considered the most primitive group of fungi. They are mostly aquatic, and their gametes are the only fungal cells known to have flagella. They reproduce both sexually and asexually; the asexual spores are called zoospores. Zygomycota (conjugated fungi) produce non-septated hyphae with many nuclei. Their hyphae fuse during sexual reproduction to produce a zygospore in a zygosporangium. Ascomycota (sac fungi) form spores in sacs called asci during sexual reproduction. Asexual reproduction is their most common form of reproduction. Basidiomycota (club fungi) produce showy fruiting bodies that contain basidia in the form of clubs. Spores are stored in the basidia. Most familiar mushrooms belong to this division. Fungi that have no known sexual cycle were classified in the form phylum Deuteromycota, which the present classification puts in the phyla Ascomycota and Basidiomycota. Glomeromycota form tight associations (called mycorrhizae) with the roots of plants.

Art Connections

Exercise:

Problem: [link] Which of the following statements is true?

    a. A dikaryotic ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
    b. A diploid ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
    c. A haploid zygote that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
    d. A dikaryotic ascus that forms in the ascocarp undergoes plasmogamy, meiosis, and mitosis to form eight ascospores.

Solution:

[link] A

**Exercise:**

Problem: [link] Which of the following statements is true?

    a. A basidium is the fruiting body of a mushroom-producing fungus, and it forms four basidiocarps.
    b. The result of the plasmogamy step is four basidiospores.
    c. Karyogamy results directly in the formation of mycelia.
    d. A basidiocarp is the fruiting body of a mushroom-producing fungus.

Solution:

[link] D

Review Questions

Exercise:

Problem: The most primitive phylum of fungi is the _____.

    a. Chytridiomycota
    b. Zygomycota
    c. Glomeromycota
    d. Ascomycota

Solution:

A

Exercise:

Problem:

Members of which phylum produce a club-shaped structure that contains spores?

a. Chytridiomycota
b. Basidiomycota
c. Glomeromycota
d. Ascomycota

Solution:

B

Exercise:

Problem:

Members of which phylum establish a successful symbiotic relationship with the roots of trees?

a. Ascomycota
b. Deuteromycota
c. Basidiomycota
d. Glomeromycota

Solution:

D

Exercise:

Problem:

The fungi that do not reproduce sexually use to be classified as _____.

a. Ascomycota
b. Deuteromycota
c. Basidiomycota
d. Glomeromycota

Solution:

B

Free Response

Exercise:

Problem:

What is the advantage for a basidiomycete to produce a showy and fleshy fruiting body?

Solution:

By ingesting spores and disseminating them in the environment as waste, animals act as agents of dispersal. The benefit to the fungus outweighs the cost of producing fleshy fruiting bodies.

Exercise:

Problem:

For each of the four groups of perfect fungi (Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota), compare the body structure and features, and provide an example.

Solution:

Chytridiomycota (Chytrids) may have a unicellular or multicellular body structure; some are aquatic with motile spores with flagella; an example is the *Allomyces*. Zygomycota (conjugated fungi) have a multicellular body structure; features include zygospores and presence in soil; examples are bread and fruit molds. Ascomycota (sac fungi) may have unicellular or multicellular body structure; a feature is sexual spores in sacs (asci); examples include the yeasts used in bread, wine, and beer production. Basidiomycota (club fungi) have multicellular bodies; features includes sexual spores in the basidiocarp (mushroom) and that they are mostly decomposers; mushroom-producing fungi are an example.

Glossary

Arbuscular mycorrhizae
    mycorrhizae commonly involving Glomeromycetes in which the
    fungal hyphae penetrate the cell walls of the plant root cells (but not
    the cell membranes)

ascocarp
    fruiting body of ascomycetes

Ascomycota
    (also, sac fungi) phylum of fungi that store spores in a sac called ascus

basidiocarp
    fruiting body that protrudes from the ground and bears the basidia

Basidiomycota
    (also, club fungi) phylum of fungi that produce club-shaped structures
    (basidia) that contain spores

basidium
    club-shaped fruiting body of basidiomycetes

Chytridiomycota
    (also, chytrids) primitive phylum of fungi that live in water and
    produce gametes with flagella

Deuteromycota
    former form phylum of fungi that do not have a known sexual
    reproductive cycle (presently members of two phyla: Ascomycota and
    Basidiomycota)

Ectomycorrhizae
    mycorrhizae in which the fungal hyphae do not penetrate the root cells
    of the plant

Glomeromycota

phylum of fungi that form symbiotic relationships with the roots of trees

mold
    tangle of visible mycelia with a fuzzy appearance

Zygomycota
    (also, conjugated fungi) phylum of fungi that form a zygote contained in a zygospore

zygospore
    structure with thick cell wall that contains the zygote in zygomycetes

Ecology of Fungi
By the end of this section, you will be able to:

- Describe the role of fungi in the ecosystem
- Describe mutualistic relationships of fungi with plant roots and photosynthetic organisms
- Describe the beneficial relationship between some fungi and insects

Fungi play a crucial role in the balance of ecosystems. They colonize most habitats on Earth, preferring dark, moist conditions. They can thrive in seemingly hostile environments, such as the tundra, thanks to a most successful symbiosis with photosynthetic organisms like algae to produce lichens. Fungi are not obvious in the way large animals or tall trees appear. Yet, like bacteria, they are the major decomposers of nature. With their versatile metabolism, fungi break down organic matter, which would not otherwise be recycled.

Habitats

Although fungi are primarily associated with humid and cool environments that provide a supply of organic matter, they colonize a surprising diversity of habitats, from seawater to human skin and mucous membranes. Chytrids are found primarily in aquatic environments. Other fungi, such as *Coccidioides immitis*, which causes pneumonia when its spores are inhaled, thrive in the dry and sandy soil of the southwestern United States. Fungi that parasitize coral reefs live in the ocean. However, most members of the Kingdom Fungi grow on the forest floor, where the dark and damp environment is rich in decaying debris from plants and animals. In these environments, fungi play a major role as decomposers and recyclers, making it possible for members of the other kingdoms to be supplied with nutrients and live.

Decomposers and Recyclers

The food web would be incomplete without organisms that decompose organic matter ([link]). Some elements—such as nitrogen and phosphorus—are required in large quantities by biological systems, and yet are not

abundant in the environment. The action of fungi releases these elements from decaying matter, making them available to other living organisms. Trace elements present in low amounts in many habitats are essential for growth, and would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.

Fungi are an important part of ecosystem nutrient cycles. These bracket fungi growing on the side of a tree are the fruiting structures of a basidiomycete. They receive their nutrients through their hyphae, which invade and decay the tree trunk.
(credit: Cory Zanker)

The ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. As seen earlier, digestion precedes ingestion. Fungi produce a variety of exoenzymes to digest nutrients. The enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Large molecules are broken down into small molecules, which are transported into the cell by a system of protein carriers embedded in the cell membrane. Because the movement of small molecules and enzymes is

dependent on the presence of water, active growth depends on a relatively high percentage of moisture in the environment.

As saprobes, fungi help maintain a sustainable ecosystem for the animals and plants that share the same habitat. In addition to replenishing the environment with nutrients, fungi interact directly with other organisms in beneficial, and sometimes damaging, ways ([link]).

Shelf fungi, so called because they grow on trees in a stack, attack and digest the trunk or branches of a tree. While some shelf fungi are found only on dead trees, others can parasitize living trees and cause eventual death, so they are considered serious tree pathogens. (credit: Cory Zanker)

Mutualistic Relationships

Symbiosis is the ecological interaction between two organisms that live together. The definition does not describe the quality of the interaction. When both members of the association benefit, the symbiotic relationship is

called mutualistic. Fungi form mutualistic associations with many types of organisms, including cyanobacteria, algae, plants, and animals.

Fungus/Plant Mutualism

One of the most remarkable associations between fungi and plants is the establishment of mycorrhizae. **Mycorrhiza**, which comes from the Greek words *myco* meaning fungus and *rhizo* meaning root, refers to the association between vascular plant roots and their symbiotic fungi. Somewhere between 80 and 90 percent of all plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

There are a number of types of mycorrhizae. **Ectomycorrhizae** ("outside" mycorrhiza) depend on fungi enveloping the roots in a sheath (called a mantle) and a Hartig net of hyphae that extends into the roots between cells ([link]). The fungal partner can belong to the Ascomycota, Basidiomycota or Zygomycota. In a second type, the Glomeromycete fungi form vesicular–arbuscular interactions with **arbuscular mycorrhiza** (sometimes called endomycorrhizae). In these mycorrhiza, the fungi form arbuscules that penetrate root cells and are the site of the metabolic exchanges between the fungus and the host plant ([link] and [link]). The arbuscules (from the Latin for little trees) have a shrub-like appearance. Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that form small seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their lifecycle.

Note:
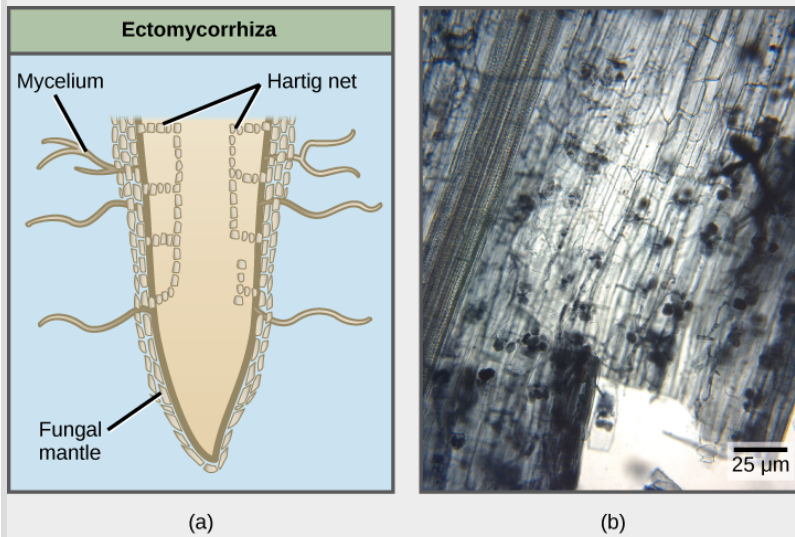
(a) Ectomycorrhiza and (b) arbuscular mycorrhiza have different mechanisms for interacting with the roots of plants. (credit b: MS Turmel, University of Manitoba, Plant Science Department)

If symbiotic fungi are absent from the soil, what impact do you think this would have on plant growth?

The (a) infection of *Pinus radiata* (Monterey pine) roots by the hyphae of *Amanita muscaria* (fly amanita) causes the pine tree to produce many small, branched rootlets.

The *Amanita* hyphae cover these small roots with a white mantle. (b) Spores (round bodies) and hyphae (thread-like structures) are evident in this light micrograph of an arbuscular mycorrhiza between a fungus and the root of a corn plant. (credit a: modification of work by Randy Molina, USDA; credit b: modification of work by Sara Wright, USDA-ARS; scale-bar data from Matt Russell)

Other examples of fungus–plant mutualism include the endophytes: fungi that live inside tissue without damaging the host plant. Endophytes release toxins that repel herbivores, or confer resistance to environmental stress factors, such as infection by microorganisms, drought, or heavy metals in soil.

Note:
Evolution Connection
Coevolution of Land Plants and Mycorrhizae
Mycorrhizae are the mutually beneficial symbiotic association between roots of vascular plants and fungi. A well-accepted theory proposes that fungi were instrumental in the evolution of the root system in plants and contributed to the success of Angiosperms. The bryophytes (mosses and liverworts), which are considered the most primitive plants and the first to survive on dry land, do not have a true root system; some have vesicular–arbuscular mycorrhizae and some do not. They depend on a simple rhizoid (an underground organ) and cannot survive in dry areas. True roots appeared in vascular plants. Vascular plants that developed a system of thin extensions from the rhizoids (found in mosses) are thought to have had a selective advantage because they had a greater surface area of contact with the fungal partners than the mosses and liverworts, thus availing themselves of more nutrients in the ground.
Fossil records indicate that fungi preceded plants on dry land. The first association between fungi and photosynthetic organisms on land involved moss-like plants and endophytes. These early associations developed

before roots appeared in plants. Slowly, the benefits of the endophyte and rhizoid interactions for both partners led to present-day mycorrhizae; up to about 90 percent of today's vascular plants have associations with fungi in their rhizosphere. The fungi involved in mycorrhizae display many characteristics of primitive fungi; they produce simple spores, show little diversification, do not have a sexual reproductive cycle, and cannot live outside of a mycorrhizal association. The plants benefited from the association because mycorrhizae allowed them to move into new habitats because of increased uptake of nutrients, and this gave them a selective advantage over plants that did not establish symbiotic relationships.

Lichens

Lichens display a range of colors and textures ([link]) and can survive in the most unusual and hostile habitats. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought, when they become completely desiccated, and then rapidly become active once water is available again.

Note:
Link to Learning

Explore the world of lichens using this site from Oregon State University.

Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like. (credit a: modification of work by Jo Naylor; credit b: modification of work by "djpmapleferryman"/Flickr; credit c: modification of work by Cory Zanker)
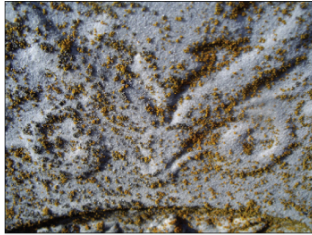
(a)   (b)   (c)

Lichens are not a single organism, but rather an example of a mutualism, in which a fungus (usually a member of the Ascomycota or Basidiomycota phyla) lives in close contact with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium) ([link]). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship. The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. Some cyanobacteria fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the symbiotic organism to the substrate.
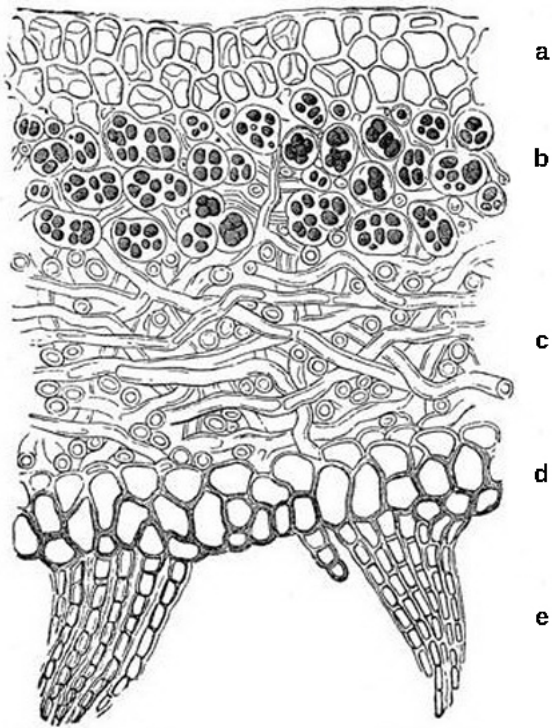
This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) rhizines to anchor the thallus to the substrate.

The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units for reproduction. Lichens produce **soredia**, clusters of algal cells surrounded by mycelia. Soredia are dispersed by wind and water and form new lichens.

Lichens are extremely sensitive to air pollution, especially to abnormal levels of nitrogen and sulfur. The U.S. Forest Service and National Park Service can monitor air quality by measuring the relative abundance and health of the lichen population in an area. Lichens fulfill many ecological roles. Caribou and reindeer eat lichens, and they provide cover for small invertebrates that hide in the mycelium. In the production of textiles, weavers used lichens to dye wool for many centuries until the advent of synthetic dyes.

Fungus/Animal Mutualism

Fungi have evolved mutualisms with numerous insects in Phylum Arthropoda: jointed, legged invertebrates. Arthropods depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus. In a second example, leaf-cutting ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in gardens ([link]). Fungi are cultivated in these disk gardens,

digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from the association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

A leaf cutting ant transports a leaf
that will feed a farmed fungus.
(credit: Scott Bauer, USDA-ARS)

Fungivores

Animal dispersal is important for some fungi because an animal may carry spores considerable distances from the source. Fungal spores are rarely completely degraded in the gastrointestinal tract of an animal, and many are able to germinate when they are passed in the feces. Some dung fungi actually require passage through the digestive system of herbivores to complete their lifecycle. The black truffle—a prized gourmet delicacy—is the fruiting body of an underground mushroom. Almost all truffles are

ectomycorrhizal, and are usually found in close association with trees. Animals eat truffles and disperse the spores. In Italy and France, truffle hunters use female pigs to sniff out truffles. Female pigs are attracted to truffles because the fungus releases a volatile compound closely related to a pheromone produced by male pigs.

Section Summary

Fungi have colonized nearly all environments on Earth, but are frequently found in cool, dark, moist places with a supply of decaying material. Fungi are saprobes that decompose organic matter. Many successful mutualistic relationships involve a fungus and another organism. Many fungi establish complex mycorrhizal associations with the roots of plants. Some ants farm fungi as a supply of food. Lichens are a symbiotic relationship between a fungus and a photosynthetic organism, usually an alga or cyanobacterium. The photosynthetic organism provides energy derived from light and carbohydrates, while the fungus supplies minerals and protection. Some animals that consume fungi help disseminate spores over long distances.

Art Connections

Exercise:

   Problem:

[link] If symbiotic fungi are absent from the soil, what impact do you think this would have on plant growth?

   Solution:

[link] Without mycorrhiza, plants cannot absorb adequate nutrients, which stunts their growth. Addition of fungal spores to sterile soil can alleviate this problem.

Review Questions

Exercise:

Problem:

What term describes the close association of a fungus with the root of a tree?

   a. a rhizoid
   b. a lichen
   c. a mycorrhiza
   d. an endophyte

Solution:

C

Exercise:

Problem: Why are fungi important decomposers?

   a. They produce many spores.
   b. They can grow in many different environments.
   c. They produce mycelia.
   d. They recycle carbon and inorganic minerals by the process of decomposition.

Solution:

D

Free Response

Exercise:

Problem:

Why does protection from light actually benefit the photosynthetic partner in lichens?

Solution:

Protection from excess light that may bleach photosynthetic pigments allows the photosynthetic partner to survive in environments unfavorable to plants.

Glossary

arbuscular mycorrhiza
  mycorrhizal association in which the fungal hyphae enter the root cells and form extensive networks

ectomycorrhiza
  mycorrhizal fungi that surround the roots with a mantle and have a Hartig net that extends into the roots between cells

lichen
  close association of a fungus with a photosynthetic alga or bacterium that benefits both partners

mycorrhiza
  mutualistic association between fungi and vascular plant roots

soredia
  clusters of algal cells and mycelia that allow lichens to propagate

Fungal Parasites and Pathogens
By the end of this section, you will be able to:

- Describe fungal parasites and pathogens of plants
- Describe the different types of fungal infections in humans
- Explain why antifungal therapy is hampered by the similarity between fungal and animal cells

Parasitism describes a symbiotic relationship in which one member of the association benefits at the expense of the other. Both parasites and pathogens harm the host; however, the pathogen causes a disease, whereas the parasite usually does not. **Commensalism** occurs when one member benefits without affecting the other.

Plant Parasites and Pathogens

The production of sufficient good-quality crops is essential to human existence. Plant diseases have ruined crops, bringing widespread famine. Many plant pathogens are fungi that cause tissue decay and eventual death of the host ([link]). In addition to destroying plant tissue directly, some plant pathogens spoil crops by producing potent toxins. Fungi are also responsible for food spoilage and the rotting of stored crops. For example, the fungus *Claviceps purpurea* causes ergot, a disease of cereal crops (especially of rye). Although the fungus reduces the yield of cereals, the effects of the ergot's alkaloid toxins on humans and animals are of much greater significance. In animals, the disease is referred to as ergotism. The most common signs and symptoms are convulsions, hallucination, gangrene, and loss of milk in cattle. The active ingredient of ergot is lysergic acid, which is a precursor of the drug LSD. Smuts, rusts, and powdery or downy mildew are other examples of common fungal pathogens that affect crops.

Some fungal pathogens include (a) green mold on grapefruit, (b) powdery mildew on a zinnia, (c) stem rust on a sheaf of barley, and (d) grey rot on grapes. In wet conditions *Botrytis cinerea,* the fungus that

causes grey rot, can destroy a grape crop. However, controlled infection of grapes by *Botrytis* results in noble rot, a condition that produces strong and much-prized dessert wines. (credit a: modification of work by Scott Bauer, USDA-ARS; credit b: modification of work by Stephen Ausmus, USDA-ARS; credit c: modification of work by David Marshall, USDA-ARS; credit d: modification of work by Joseph Smilanick, USDA-ARS)

(a)

(b)

(c)

(d)

Aflatoxins are toxic, carcinogenic compounds released by fungi of the genus *Aspergillus*. Periodically, harvests of nuts and grains are tainted by aflatoxins, leading to massive recall of produce. This sometimes ruins producers and causes food shortages in developing countries.

Animal and Human Parasites and Pathogens

Fungi can affect animals, including humans, in several ways. A **mycosis** is a fungal disease that results from infection and direct damage. Fungi attack animals directly by colonizing and destroying tissues. **Mycotoxicosis** is the

poisoning of humans (and other animals) by foods contaminated by fungal toxins (mycotoxins). **Mycetismus** describes the ingestion of preformed toxins in poisonous mushrooms. In addition, individuals who display hypersensitivity to molds and spores develop strong and dangerous allergic reactions. Fungal infections are generally very difficult to treat because, unlike bacteria, fungi are eukaryotes. Antibiotics only target prokaryotic cells, whereas compounds that kill fungi also harm the eukaryotic animal host.

Many fungal infections are superficial; that is, they occur on the animal's skin. Termed cutaneous ("skin") mycoses, they can have devastating effects. For example, the decline of the world's frog population in recent years may be caused by the chytrid fungus *Batrachochytrium dendrobatidis,* which infects the skin of frogs and presumably interferes with gaseous exchange. Similarly, more than a million bats in the United States have been killed by white-nose syndrome, which appears as a white ring around the mouth of the bat. It is caused by the cold-loving fungus *Pseudogymnoascus destructans*, which disseminates its deadly spores in caves where bats hibernate. Mycologists are researching the transmission, mechanism, and control of *P. destructans* to stop its spread.

Fungi that cause the superficial mycoses of the epidermis, hair, and nails rarely spread to the underlying tissue ([link]). These fungi are often misnamed "dermatophytes", from the Greek words *dermis* meaning skin and *phyte* meaning plant, although they are not plants. Dermatophytes are also called "ringworms" because of the red ring they cause on skin. They secrete extracellular enzymes that break down keratin (a protein found in hair, skin, and nails), causing conditions such as athlete's foot and jock itch. These conditions are usually treated with over-the-counter topical creams and powders, and are easily cleared. More persistent superficial mycoses may require prescription oral medications.

(a) Ringworm presents as a red ring on skin; (b) *Trichophyton violaceum*, shown in this bright field light micrograph, causes superficial mycoses on the scalp; (c) *Histoplasma capsulatum* is an

ascomycete that infects airways and causes symptoms similar to influenza. (credit a: modification of work by Dr. Lucille K. Georg, CDC; credit b: modification of work by Dr. Lucille K. Georg, CDC; credit c: modification of work by M. Renz, CDC; scale-bar data from Matt Russell)

(a)   (b)   (c)
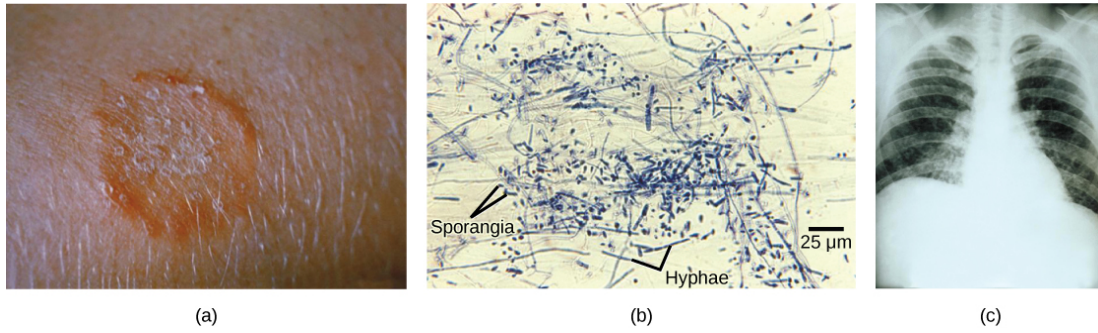
Systemic mycoses spread to internal organs, most commonly entering the body through the respiratory system. For example, coccidioidomycosis (valley fever) is commonly found in the southwestern United States, where the fungus resides in the dust. Once inhaled, the spores develop in the lungs and cause symptoms similar to those of tuberculosis. Histoplasmosis is caused by the dimorphic fungus *Histoplasma capsulatum*. It also causes pulmonary infections, and in rarer cases, swelling of the membranes of the brain and spinal cord. Treatment of these and many other fungal diseases requires the use of antifungal medications that have serious side effects.

Opportunistic mycoses are fungal infections that are either common in all environments, or part of the normal biota. They mainly affect individuals who have a compromised immune system. Patients in the late stages of AIDS suffer from opportunistic mycoses that can be life threatening. The yeast *Candida* sp., a common member of the natural biota, can grow unchecked and infect the vagina or mouth (oral thrush) if the pH of the surrounding environment, the person's immune defenses, or the normal population of bacteria are altered.

Mycetismus can occur when poisonous mushrooms are eaten. It causes a number of human fatalities during mushroom-picking season. Many edible fruiting bodies of fungi resemble highly poisonous relatives, and amateur mushroom hunters are cautioned to carefully inspect their harvest and avoid

eating mushrooms of doubtful origin. The adage "there are bold mushroom pickers and old mushroom pickers, but are there no old, bold mushroom pickers" is unfortunately true.

Note:
Scientific Method Connection
Dutch Elm Disease
Question: Do trees resistant to Dutch elm disease secrete antifungal compounds?
Hypothesis: Construct a hypothesis that addresses this question.
Background: Dutch elm disease is a fungal infestation that affects many species of elm (*Ulmus*) in North America. The fungus infects the vascular system of the tree, which blocks water flow within the plant and mimics drought stress. Accidently introduced to the United States in the early 1930s, it decimated shade trees across the continent. It is caused by the fungus *Ophiostoma ulmi*. The elm bark beetle acts as a vector and transmits the disease from tree to tree. Many European and Asiatic elms are less susceptible to the disease than are American elms.
Test the hypothesis: A researcher testing this hypothesis might do the following. Inoculate several Petri plates containing a medium that supports the growth of fungi with fragments of *Ophiostoma* mycelium. Cut (with a metal punch) several disks from the vascular tissue of susceptible varieties of American elms and resistant European and Asiatic elms. Include control Petri plates inoculated with mycelia without plant tissue to verify that the medium and incubation conditions do not interfere with fungal growth. As a positive control, add paper disks impregnated with a known fungicide to Petri plates inoculated with the mycelium.
Incubate the plates for a set number of days to allow fungal growth and spreading of the mycelium over the surface of the plate. Record the diameter of the zone of clearing, if any, around the tissue samples and the fungicide control disk.
Record your observations in the following table.

Results of Antifungal Testing of Vascular Tissue from Different Species of Elm	
Disk	**Zone of Inhibition (mm)**
Distilled Water	
Fungicide	
Tissue from Susceptible Elm #1	
Tissue from Susceptible Elm #2	
Tissue from Resistant Elm #1	
Tissue from Resistant Elm #2	

Analyze the data and report the results. Compare the effect of distilled water to the fungicide. These are negative and positive controls that validate the experimental set up. The fungicide should be surrounded by a clear zone where the fungus growth was inhibited. Is there a difference among different species of elm?
Draw a conclusion: Was there antifungal activity as expected from the fungicide? Did the results support the hypothesis? If not, how can this be explained? There are several possible explanations for resistance to a pathogen. Active deterrence of infection is only one of them.

Section Summary

Fungi establish parasitic relationships with plants and animals. Fungal diseases can decimate crops and spoil food during storage. Compounds produced by fungi can be toxic to humans and other animals. Mycoses are infections caused by fungi. Superficial mycoses affect the skin, whereas

systemic mycoses spread through the body. Fungal infections are difficult to cure.

Review Questions

Exercise:

Problem:

A fungus that climbs up a tree reaching higher elevation to release its spores in the wind and does not receive any nutrients from the tree or contribute to the tree's welfare is described as a _____.

   a. commensal
   b. mutualist
   c. parasite
   d. pathogen

Solution:

A

Exercise:

Problem:

A fungal infection that affects nails and skin is classified as _____.

   a. systemic mycosis
   b. mycetismus
   c. superficial mycosis
   d. mycotoxicosis

Solution:

C

Free Response

Exercise:

Problem:

Why can superficial mycoses in humans lead to bacterial infections?

Solution:

Dermatophytes that colonize skin break down the keratinized layer of dead cells that protects tissues from bacterial invasion. Once the integrity of the skin is breached, bacteria can enter the deeper layers of tissues and cause infections.

Glossary

commensalism
> symbiotic relationship in which one member benefits while the other member is not affected

mycetismus
> ingestion of toxins in poisonous mushrooms

mycosis
> fungal infection

mycotoxicosis
> poisoning by a fungal toxin released in food

parasitism
> symbiotic relationship in which one member of the association benefits at the expense of the other

Importance of Fungi in Human Life
By the end of this section, you will be able to:

- Describe the importance of fungi to the balance of the environment
- Summarize the role of fungi in food and beverage preparation
- Describe the importance of fungi in the chemical and pharmaceutical industries
- Discuss the role of fungi as model organisms

Although we often think of fungi as organisms that cause disease and rot food, fungi are important to human life on many levels. As we have seen, they influence the well-being of human populations on a large scale because they are part of the nutrient cycle in ecosystems. They have other ecosystem roles as well. As animal pathogens, fungi help to control the population of damaging pests. These fungi are very specific to the insects they attack, and do not infect animals or plants. Fungi are currently under investigation as potential microbial insecticides, with several already on the market. For example, the fungus *Beauveria bassiana* is a pesticide being tested as a possible biological control agent for the recent spread of emerald ash borer. It has been released in Michigan, Illinois, Indiana, Ohio, West Virginia and Maryland ([link]).

The emerald ash borer is an insect that attacks ash trees. It is in turn parasitized by a pathogenic fungus

The mycorrhizal relationship between fungi and plant roots is essential for the productivity of farm land. Without the fungal partner in root systems, 80–90 percent of trees and grasses would not survive. Mycorrhizal fungal inoculants are available as soil amendments from gardening supply stores and are promoted by supporters of organic agriculture.

We also eat some types of fungi. Mushrooms figure prominently in the human diet. Morels, shiitake mushrooms, chanterelles, and truffles are considered delicacies ([link]). The humble meadow mushroom, *Agaricus campestris*, appears in many dishes. Molds of the genus *Penicillium* ripen many cheeses. They originate in the natural environment such as the caves of Roquefort, France, where wheels of sheep milk cheese are stacked in order to capture the molds responsible for the blue veins and pungent taste of the cheese.

The morel mushroom is an ascomycete much appreciated for its delicate taste. (credit: Jason Hollinger)

Fermentation—of grains to produce beer, and of fruits to produce wine—is an ancient art that humans in most cultures have practiced for millennia. Wild yeasts are acquired from the environment and used to ferment sugars into CO_2 and ethyl alcohol under anaerobic conditions. It is now possible to purchase isolated strains of wild yeasts from different wine-making regions. Louis Pasteur was instrumental in developing a reliable strain of brewer's yeast, *Saccharomyces cerevisiae*, for the French brewing industry in the late 1850s. This was one of the first examples of biotechnology patenting.

Many secondary metabolites of fungi are of great commercial importance. Antibiotics are naturally produced by fungi to kill or inhibit the growth of bacteria, limiting their competition in the natural environment. Important antibiotics, such as penicillin and the cephalosporins, are isolated from fungi. Valuable drugs isolated from fungi include the immunosuppressant drug cyclosporine (which reduces the risk of rejection after organ transplant), the precursors of steroid hormones, and ergot alkaloids used to stop bleeding. Psilocybin is a compound found in fungi such as *Psilocybe semilanceata* and *Gymnopilus junonius*, which have been used for their hallucinogenic properties by various cultures for thousands of years.

As simple eukaryotic organisms, fungi are important model research organisms. Many advances in modern genetics were achieved by the use of the red bread mold *Neurospora crassa*. Additionally, many important genes originally discovered in *S. cerevisiae* served as a starting point in discovering analogous human genes. As a eukaryotic organism, the yeast cell produces and modifies proteins in a manner similar to human cells, as opposed to the bacterium *Escherichia coli*, which lacks the internal membrane structures and enzymes to tag proteins for export. This makes yeast a much better organism for use in recombinant DNA technology

experiments. Like bacteria, yeasts grow easily in culture, have a short generation time, and are amenable to genetic modification.

Section Summary

Fungi are important to everyday human life. Fungi are important decomposers in most ecosystems. Mycorrhizal fungi are essential for the growth of most plants. Fungi, as food, play a role in human nutrition in the form of mushrooms, and also as agents of fermentation in the production of bread, cheeses, alcoholic beverages, and numerous other food preparations. Secondary metabolites of fungi are used as medicines, such as antibiotics and anticoagulants. Fungi are model organisms for the study of eukaryotic genetics and metabolism.

Review Questions

Exercise:

Problem:

Yeast is a facultative anaerobe. This means that alcohol fermentation takes place only if:

   a. the temperature is close to 37°C
   b. the atmosphere does not contain oxygen
   c. sugar is provided to the cells
   d. light is provided to the cells

Solution:

B

Exercise:

Problem:

The advantage of yeast cells over bacterial cells to express human proteins is that:

a. yeast cells grow faster
b. yeast cells are easier to manipulate genetically
c. yeast cells are eukaryotic and modify proteins similarly to human cells
d. yeast cells are easily lysed to purify the proteins

Solution:

C

Free Response

Exercise:

Problem:

Historically, artisanal breads were produced by capturing wild yeasts from the air. Prior to the development of modern yeast strains, the production of artisanal breads was long and laborious because many batches of dough ended up being discarded. Can you explain this fact?

Solution:

The dough is often contaminated by toxic spores that float in the air. It was one of Louis Pasteur's achievements to purify reliable strains of baker's yeast to produce bread consistently.

Introduction
class="introduction"

Seedless plants, like these horsetails (*Equisetum* sp.), thrive in damp, shaded environments under a tree canopy where dryness is rare. (credit: modification of work by Jerry Kirkhart)

An incredible variety of seedless plants populates the terrestrial landscape. Mosses may grow on a tree trunk, and horsetails may display their jointed stems and spindly leaves across the forest floor. Today, seedless plants represent only a small fraction of the plants in our environment; yet, three hundred million years ago, seedless plants dominated the landscape and grew in the enormous swampy forests of the Carboniferous period. Their decomposition created large deposits of coal that we mine today.

Current evolutionary thought holds that all plants—green algae as well as land dwellers—are monophyletic; that is, they are descendants of a single common ancestor. The evolutionary transition from water to land imposed severe constraints on plants. They had to develop strategies to avoid drying out, to disperse reproductive cells in air, for structural support, and for capturing and filtering sunlight. While seed plants developed adaptations that allowed them to populate even the most arid habitats on Earth, full independence from water did not happen in all plants. Most seedless plants still require a moist environment.

Early Plant Life
By the end of this section, you will be able to:

- Discuss the challenges to plant life on land
- Describe the adaptations that allowed plants to colonize the land
- Describe the timeline of plant evolution and the impact of land plants on other living things

The kingdom Plantae constitutes large and varied groups of organisms. There are more than 300,000 species of catalogued plants. Of these, more than 260,000 are seed plants. Mosses, ferns, conifers, and flowering plants are all members of the plant kingdom. Most biologists also consider green algae to be plants, although others exclude all algae from the plant kingdom. The reason for this disagreement stems from the fact that only green algae, the **Charophytes**, share common characteristics with land plants (such as using chlorophyll *a* and *b* plus carotene in the same proportion as plants). These characteristics are absent in other types of algae.

Note:
Evolution Connection
Algae and Evolutionary Paths to Photosynthesis
Some scientists consider all algae to be plants, while others assert that only the Charophytes belong in the kingdom Plantae. These divergent opinions are related to the different evolutionary paths to photosynthesis selected for in different types of algae. While all algae are photosynthetic—that is, they contain some form of a chloroplast—they didn't all become photosynthetic via the same path.
The ancestors to the green algae became photosynthetic by endosymbiosing a green, photosynthetic bacterium about 1.65 billion years ago. That algal line evolved into the Charophytes, and eventually into the modern mosses, ferns, gymnosperms, and angiosperms. Their evolutionary trajectory was relatively straight and monophyletic. In contrast, the other algae—red, brown, golden, stramenopiles, and so on—all became photosynthetic by secondary, or even tertiary, endosymbiotic events; that is, they endosymbiosed cells that had already endosymbiosed a

cyanobacterium. These latecomers to photosynthesis are parallels to the Charophytes in terms of autotrophy, but they did not expand to the same extent as the Charophytes, nor did they colonize the land.

The different views on whether all algae are Plantae arise from how these evolutionary paths are viewed. Scientists who solely track evolutionary straight lines (that is, monophyly), consider only the Charophytes as plants. To biologists who cast a broad net over living things that share a common characteristic (in this case, photosynthetic eukaryotes), all algae are plants.

Note:
Link to Learning

Go to this [interactive website](#) to get a more in-depth view of the Charophytes.

Plant Adaptations to Life on Land

As organisms adapted to life on land, they had to contend with several challenges in the terrestrial environment. Water has been described as "the stuff of life." The cell's interior is a watery soup: in this medium, most small molecules dissolve and diffuse, and the majority of the chemical reactions of metabolism take place. Desiccation, or drying out, is a constant danger for an organism exposed to air. Even when parts of a plant are close to a source of water, the aerial structures are likely to dry out. Water also provides buoyancy to organisms. On land, plants need to develop structural support in a medium that does not give the same lift as water. The organism is also subject to bombardment by mutagenic radiation, because air does not

filter out ultraviolet rays of sunlight. Additionally, the male gametes must reach the female gametes using new strategies, because swimming is no longer possible. Therefore, both gametes and zygotes must be protected from desiccation. The successful land plants developed strategies to deal with all of these challenges. Not all adaptations appeared at once. Some species never moved very far from the aquatic environment, whereas others went on to conquer the driest environments on Earth.

To balance these survival challenges, life on land offers several advantages. First, sunlight is abundant. Water acts as a filter, altering the spectral quality of light absorbed by the photosynthetic pigment chlorophyll. Second, carbon dioxide is more readily available in air than in water, since it diffuses faster in air. Third, land plants evolved before land animals; therefore, until dry land was colonized by animals, no predators threatened plant life. This situation changed as animals emerged from the water and fed on the abundant sources of nutrients in the established flora. In turn, plants developed strategies to deter predation: from spines and thorns to toxic chemicals.

Early land plants, like the early land animals, did not live very far from an abundant source of water and developed survival strategies to combat dryness. One of these strategies is called tolerance. Many mosses, for example, can dry out to a brown and brittle mat, but as soon as rain or a flood makes water available, mosses will absorb it and are restored to their healthy green appearance. Another strategy is to colonize environments with high humidity, where droughts are uncommon. Ferns, which are considered an early lineage of plants, thrive in damp and cool places such as the understory of temperate forests. Later, plants moved away from moist or aquatic environments using resistance to desiccation, rather than tolerance. These plants, like cacti, minimize the loss of water to such an extent they can survive in extremely dry environments.

The most successful adaptation solution was the development of new structures that gave plants the advantage when colonizing new and dry environments. Four major adaptations are found in all terrestrial plants: the alternation of generations, a sporangium in which the spores are formed, a gametangium that produces haploid cells, and apical meristem tissue in

roots and shoots. The evolution of a waxy cuticle and a cell wall with lignin also contributed to the success of land plants. These adaptations are noticeably lacking in the closely related green algae—another reason for the debate over their placement in the plant kingdom.

Alternation of Generations

Alternation of generations describes a life cycle in which an organism has both haploid and diploid multicellular stages ([link]).
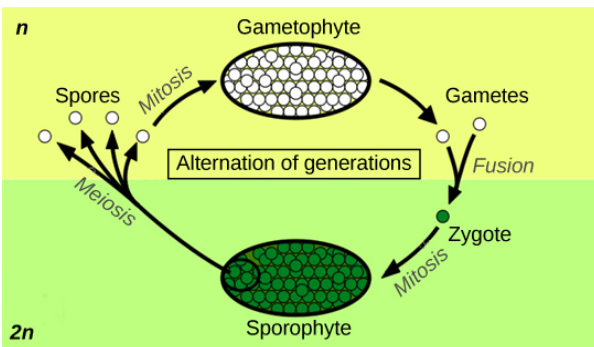
Alternation of generations between the 1n gametophyte and 2n sporophyte is shown. (credit: Peter Coxhead)

Haplontic refers to a lifecycle in which there is a dominant haploid stage, and **diplontic** refers to a lifecycle in which the diploid is the dominant life stage. Humans are diplontic. Most plants exhibit alternation of generations, which is described as **haplodiplodontic:** the haploid multicellular form, known as a gametophyte, is followed in the development sequence by a multicellular diploid organism: the sporophyte. The gametophyte gives rise to the gametes (reproductive cells) by mitosis. This can be the most obvious phase of the life cycle of the plant, as in the mosses, or it can occur in a

microscopic structure, such as a pollen grain, in the higher plants (a common collective term for the vascular plants). The sporophyte stage is barely noticeable in lower plants (the collective term for the plant groups of mosses, liverworts, and lichens). Towering trees are the diplontic phase in the lifecycles of plants such as sequoias and pines.

Protection of the embryo is a major requirement for land plants. The vulnerable embryo must be sheltered from desiccation and other environmental hazards. In both seedless and seed plants, the female gametophyte provides protection and nutrients to the embryo as it develops into the new generation of sporophyte. This distinguishing feature of land plants gave the group its alternate name of **embryophytes**.

Sporangia in Seedless Plants

The sporophyte of seedless plants is diploid and results from syngamy (fusion) of two gametes. The sporophyte bears the sporangia (singular, sporangium): organs that first appeared in the land plants. The term "sporangia" literally means "spore in a vessel," as it is a reproductive sac that contains spores [link]. Inside the multicellular sporangia, the diploid **sporocytes**, or mother cells, produce haploid spores by meiosis, where the $2n$ chromosome number is reduced to $1n$ (note that many plant sporophytes are polyploid: for example, durum wheat is tetraploid, bread wheat is hexaploid, and some ferns are 1000-ploid). The spores are later released by the sporangia and disperse in the environment. Two different types of spores are produced in land plants, resulting in the separation of sexes at different points in the lifecycle. **Seedless non-vascular plants** produce only one kind of spore and are called **homosporous**. The gametophyte phase is dominant in these plants. After germinating from a spore, the resulting gametophyte produces both male and female gametangia, usually on the same individual. In contrast, **heterosporous** plants produce two morphologically different types of spores. The male spores are called **microspores**, because of their smaller size, and develop into the male gametophyte; the comparatively larger **megaspores** develop into the female gametophyte. Heterospory is observed in a few **seedless vascular plants** and in all seed plants.

Spore-producing sacs called sporangia grow at the ends of long, thin stalks in this photo of the moss *Esporangios bryum*. (credit: Javier Martin)

When the haploid spore germinates in a hospitable environment, it generates a multicellular gametophyte by mitosis. The gametophyte supports the zygote formed from the fusion of gametes and the resulting young sporophyte (vegetative form). The cycle then begins anew.

The spores of seedless plants are surrounded by thick cell walls containing a tough polymer known as **sporopollenin**. This complex substance is characterized by long chains of organic molecules related to fatty acids and carotenoids: hence the yellow color of most pollen. Sporopollenin is unusually resistant to chemical and biological degradation. In seed plants, which use pollen to transfer the male sperm to the female egg, the toughness of sporopollenin explains the existence of well-preserved pollen fossils. Sporopollenin was once thought to be an innovation of land plants; however, the green algae *Coleochaetes* forms spores that contain sporopollenin.

Gametangia in Seedless Plants

Gametangia (singular, gametangium) are structures observed on multicellular haploid gametophytes. In the gametangia, precursor cells give rise to gametes by mitosis. The male gametangium (**antheridium**) releases sperm. Many seedless plants produce sperm equipped with flagella that enable them to swim in a moist environment to the **archegonia**: the female gametangium. The embryo develops inside the archegonium as the sporophyte. Gametangia are prominent in seedless plants, but are very rarely found in seed plants.

Apical Meristems

Shoots and roots of plants increase in length through rapid cell division in a tissue called the apical meristem, which is a small zone of cells found at the shoot tip or root tip ([link]). The apical meristem is made of undifferentiated cells that continue to proliferate throughout the life of the plant. Meristematic cells give rise to all the specialized tissues of the organism. Elongation of the shoots and roots allows a plant to access additional space and resources: light in the case of the shoot, and water and minerals in the case of roots. A separate meristem, called the lateral meristem, produces cells that increase the diameter of tree trunks.

Apical meristem
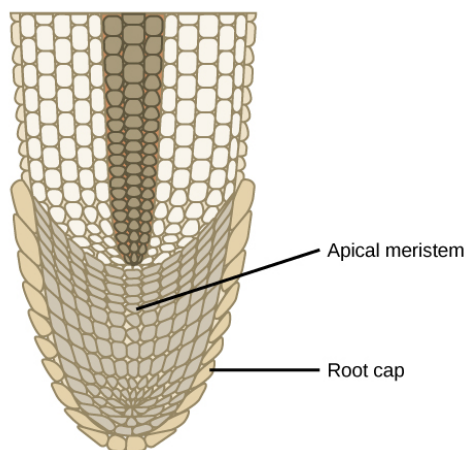
Root cap

Addition of new cells in a root occurs at the apical

meristem. Subsequent enlargement of these cells causes the organ to grow and elongate. The root cap protects the fragile apical meristem as the root tip is pushed through the soil by cell elongation.

Additional Land Plant Adaptations

As plants adapted to dry land and became independent from the constant presence of water in damp habitats, new organs and structures made their appearance. Early land plants did not grow more than a few inches off the ground, competing for light on these low mats. By developing a shoot and growing taller, individual plants captured more light. Because air offers substantially less support than water, land plants incorporated more rigid molecules in their stems (and later, tree trunks). In small plants such as single-celled algae, simple diffusion suffices to distribute water and nutrients throughout the organism. However, for plants to evolve larger forms, the evolution of vascular tissue for the distribution of water and solutes was a prerequisite. The vascular system contains xylem and phloem tissues. Xylem conducts water and minerals absorbed from the soil up to the shoot, while phloem transports food derived from photosynthesis throughout the entire plant. A root system evolved to take up water and minerals from the soil, and to anchor the increasingly taller shoot in the soil.

In land plants, a waxy, waterproof cover called a cuticle protects the leaves and stems from desiccation. However, the cuticle also prevents intake of carbon dioxide needed for the synthesis of carbohydrates through photosynthesis. To overcome this, stomata or pores that open and close to regulate traffic of gases and water vapor appeared in plants as they moved away from moist environments into drier habitats.

Water filters ultraviolet-B (UVB) light, which is harmful to all organisms, especially those that must absorb light to survive. This filtering does not occur for land plants. This presented an additional challenge to land colonization, which was met by the evolution of biosynthetic pathways for the synthesis of protective flavonoids and other compounds: pigments that absorb UV wavelengths of light and protect the aerial parts of plants from photodynamic damage.

Plants cannot avoid being eaten by animals. Instead, they synthesize a large range of poisonous secondary metabolites: complex organic molecules such as alkaloids, whose noxious smells and unpleasant taste deter animals. These toxic compounds can also cause severe diseases and even death, thus discouraging predation. Humans have used many of these compounds for centuries as drugs, medications, or spices. In contrast, as plants co-evolved with animals, the development of sweet and nutritious metabolites lured animals into providing valuable assistance in dispersing pollen grains, fruit, or seeds. Plants have been enlisting animals to be their helpers in this way for hundreds of millions of years.

Evolution of Land Plants

No discussion of the evolution of plants on land can be undertaken without a brief review of the timeline of the geological eras. The early era, known as the Paleozoic, is divided into six periods. It starts with the Cambrian period, followed by the Ordovician, Silurian, Devonian, Carboniferous, and Permian. The major event to mark the Ordovician, more than 500 million years ago, was the colonization of land by the ancestors of modern land plants. Fossilized cells, cuticles, and spores of early land plants have been dated as far back as the Ordovician period in the early Paleozoic era. The oldest-known vascular plants have been identified in deposits from the Devonian. One of the richest sources of information is the Rhynie chert, a sedimentary rock deposit found in Rhynie, Scotland ([link]), where embedded fossils of some of the earliest vascular plants have been identified.
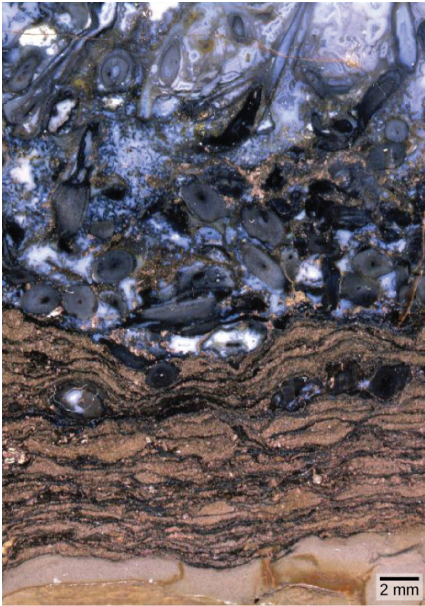
(a)   (b)

This Rhynie chert contains fossilized material from vascular plants. The area inside the circle contains bulbous underground stems called corms, and root-like structures called rhizoids. (credit b: modification of work by Peter Coxhead based on original image by "Smith609"/Wikimedia Commons; scale-bar data from Matt Russell)

Paleobotanists distinguish between **extinct** species, as fossils, and **extant** species, which are still living. The extinct vascular plants, classified as zosterophylls and trimerophytes, most probably lacked true leaves and roots and formed low vegetation mats similar in size to modern-day mosses, although some trimetophytes could reach one meter in height. The later genus *Cooksonia*, which flourished during the Silurian, has been extensively studied from well-preserved examples. Imprints of *Cooksonia* show slender branching stems ending in what appear to be sporangia. From the recovered specimens, it is not possible to establish for certain whether *Cooksonia* possessed vascular tissues. Fossils indicate that by the end of the Devonian period, ferns, horsetails, and seed plants populated the landscape, giving rising to trees and forests. This luxuriant vegetation helped enrich

the atmosphere in oxygen, making it easier for air-breathing animals to colonize dry land. Plants also established early symbiotic relationships with fungi, creating mycorrhizae: a relationship in which the fungal network of filaments increases the efficiency of the plant root system, and the plants provide the fungi with byproducts of photosynthesis.

Paleobotanists can also study fossil DNA, which can yield a large amount of information, by analyzing and comparing the DNA sequences of extinct plants with those of living and related organisms. Through this analysis, evolutionary relationships can be built for plant lineages.

Some paleobotanists are skeptical of the conclusions drawn from the analysis of molecular fossils. For example, the chemical materials of interest degrade rapidly when exposed to air during their initial isolation, as well as in further manipulations. There is always a high risk of contaminating the specimens with extraneous material, mostly from microorganisms. Nevertheless, as technology is refined, the analysis of DNA from fossilized plants will provide invaluable information on the evolution of plants and their adaptation to an ever-changing environment.

The Major Divisions of Land Plants

The green algae and land plants are grouped together into a subphylum called the Streptophytina, and thus are called Streptophytes. In a further division, land plants are classified into two major groups according to the absence or presence of vascular tissue, as detailed in [link]. Plants that lack vascular tissue, which is formed of specialized cells for the transport of water and nutrients, are referred to as **non-vascular plants**. Liverworts, mosses, and hornworts are seedless, non-vascular plants that likely appeared early in land plant evolution. Vascular plants developed a network of cells that conduct water and solutes. The first vascular plants appeared in the late Ordovician and were probably similar to lycophytes, which include club mosses (not to be confused with the mosses) and the pterophytes (ferns, horsetails, and whisk ferns). Lycophytes and pterophytes are referred to as seedless vascular plants, because they do not produce seeds. The seed plants, or spermatophytes, form the largest group of all existing plants, and hence dominate the landscape. Seed plants include gymnosperms, most notably conifers (Gymnosperms), which produce "naked seeds," and the most successful of all plants, the flowering plants (Angiosperms). Angiosperms protect their seeds inside chambers at the center of a flower; the walls of the chamber later develop into a fruit.

STREPTOPHYTES: THE GREEN PLANTS						
Charophytes	Embryophytes: The Land Plants					
	Non Vascular			Vascular		
	Seedless Plants Bryophytes			Seedless Plants		Seed Plants Spermatophytes
				Lycophytes	Pterophytes	
	Liver-worts	Horn-worts	Mosses	Club Mosses	Whisk Ferns	Gymno-sperms / Angio-sperms
				Quillworts	Horsetails	
				Spike Mosses	Ferns	

This table shows the major divisions of green plants.

Which of the following statements about plant divisions is false?

a. Lycophytes and pterophytes are seedless vascular plants.
b. All vascular plants produce seeds.
c. All nonvascular embryophytes are bryophytes.
d. Seed plants include angiosperms and gymnosperms.

Section Summary

Land plants acquired traits that made it possible to colonize land and survive out of the water. All land plants share the following characteristics: alternation of generations, with the haploid plant called a gametophyte, and the diploid plant called a sporophyte; protection of the embryo, formation of haploid spores in a sporangium, formation of gametes in a gametangium, and an apical meristem. Vascular tissues, roots, leaves, cuticle cover, and a tough outer layer that protects the spores contributed to the adaptation of plants to dry land. Land plants appeared about 500 million years ago in the Ordovician period.

Art Connections

Exercise:

Problem:

[link] Which of the following statements about plant divisions is false?

    a. Lycophytes and pterophytes are seedless vascular plants.
    b. All vascular plants produce seeds.
    c. All nonvascular embryophytes are bryophytes.
    d. Seed plants include angiosperms and gymnosperms.

Solution:

[link] B.

Review Questions

Exercise:

Problem:

The land plants are probably descendants of which of these groups?

    a. green algae
    b. red algae
    c. brown algae
    d. angiosperms

Solution:

A

Exercise:

Problem: Alternation of generations means that plants produce:

a. only haploid multicellular organisms
b. only diploid multicellular organisms
c. only diploid multicellular organisms with single-celled haploid gametes
d. both haploid and diploid multicellular organisms

Solution:

D

Exercise:

Problem:

Which of the following traits of land plants allows them to grow in height?

a. alternation of generations
b. waxy cuticle
c. tracheids
d. sporopollenin

Solution:

C

Free Response

Exercise:

Problem:

Why did land plants lose some of the accessory pigments present in brown and red algae?

Solution:

Sunlight is not filtered by water or other algae on land; therefore, there is no need to collect light at additional wavelengths made available by other pigment coloration.

Exercise:

Problem: What is the difference between extant and extinct?

Solution:

Paleobotanists distinguish between extinct species, which no longer live, and extant species, which are still living.

Glossary

antheridium
    male gametangium

archegonium
    female gametangium

charophyte
    other term for green algae; considered the closest relative of land plants

diplontic
    diploid stage is the dominant stage

embryophyte
    other name for land plant; embryo is protected and nourished by the sporophyte

extant
    still-living species

extinct
    no longer existing species

gametangium
    structure on the gametophyte in which gametes are produced

haplodiplodontic
    haploid and diploid stages alternate

haplontic
    haploid stage is the dominant stage

heterosporous
    produces two types of spores

homosporous
    produces one type of spore

megaspore
    female spore

microspore
    male spore

non-vascular plant
    plant that lacks vascular tissue, which is formed of specialized cells for
    the transport of water and nutrients

seedless vascular plant
    plant that does not produce seeds

sporocyte
    diploid cell that produces spores by meiosis

sporopollenin
    tough polymer surrounding the spore

vascular plant
    plant containing a network of cells that conducts water and solutes
    through the organism

Bryophytes
By the end of this section, you will be able to:

- Identify the main characteristics of bryophytes
- Describe the distinguishing traits of liverworts, hornworts, and mosses
- Chart the development of land adaptations in the bryophytes
- Describe the events in the bryophyte lifecycle

Bryophytes are the group of plants that are the closest extant relative of early terrestrial plants. The first bryophytes (liverworts) most likely appeared in the Ordovician period, about 450 million years ago. Because of the lack of lignin and other resistant structures, the likelihood of bryophytes forming fossils is rather small. Some spores protected by sporopollenin have survived and are attributed to early bryophytes. By the Silurian period, however, vascular plants had spread through the continents. This compelling fact is used as evidence that non-vascular plants must have preceded the Silurian period.

More than 25,000 species of bryophytes thrive in mostly damp habitats, although some live in deserts. They constitute the major flora of inhospitable environments like the tundra, where their small size and tolerance to desiccation offer distinct advantages. They generally lack lignin and do not have actual tracheids (xylem cells specialized for water conduction). Rather, water and nutrients circulate inside specialized conducting cells. Although the term non-tracheophyte is more accurate, bryophytes are commonly called nonvascular plants.

In a bryophyte, all the conspicuous vegetative organs—including the photosynthetic leaf-like structures, the thallus, stem, and the rhizoid that anchors the plant to its substrate—belong to the haploid organism or gametophyte. The sporophyte is barely noticeable. The gametes formed by bryophytes swim with a flagellum, as do gametes in a few of the tracheophytes. The sporangium—the multicellular sexual reproductive structure—is present in bryophytes and absent in the majority of algae. The bryophyte embryo also remains attached to the parent plant, which protects and nourishes it. This is a characteristic of land plants.

The bryophytes are divided into three phyla: the liverworts or Hepaticophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

Liverworts

Liverworts (Hepaticophyta) are viewed as the plants most closely related to the ancestor that moved to land. Liverworts have colonized every terrestrial habitat on Earth and diversified to more than 7000 existing species ([link]). Some gametophytes form lobate green structures, as seen in [link]. The shape is similar to the lobes of the liver, and hence provides the origin of the name given to the phylum.

This 1904 drawing shows the variety of forms of Hepaticophyta.

A liverwort, *Lunularia cruciata*, displays its lobate, flat thallus. The organism in the photograph is in the gametophyte stage.

Openings that allow the movement of gases may be observed in liverworts. However, these are not stomata, because they do not actively open and close. The plant takes up water over its entire surface and has no cuticle to prevent desiccation. [link] represents the lifecycle of a liverwort. The cycle starts with the release of haploid spores from the sporangium that developed on the sporophyte. Spores disseminated by wind or water germinate into flattened thalli attached to the substrate by thin, single-celled filaments. Male and female gametangia develop on separate, individual plants. Once released, male gametes swim with the aid of their flagella to the female gametangium (the archegonium), and fertilization ensues. The zygote grows into a small sporophyte still attached to the parent gametophyte. It will give rise, by meiosis, to the next generation of spores. Liverwort plants can also reproduce asexually, by the breaking of branches or the spreading of leaf fragments called gemmae. In this latter type of reproduction, the **gemmae** —small, intact, complete pieces of plant that are produced in a cup on the

surface of the thallus (shown in [link])—are splashed out of the cup by raindrops. The gemmae then land nearby and develop into gametophytes.
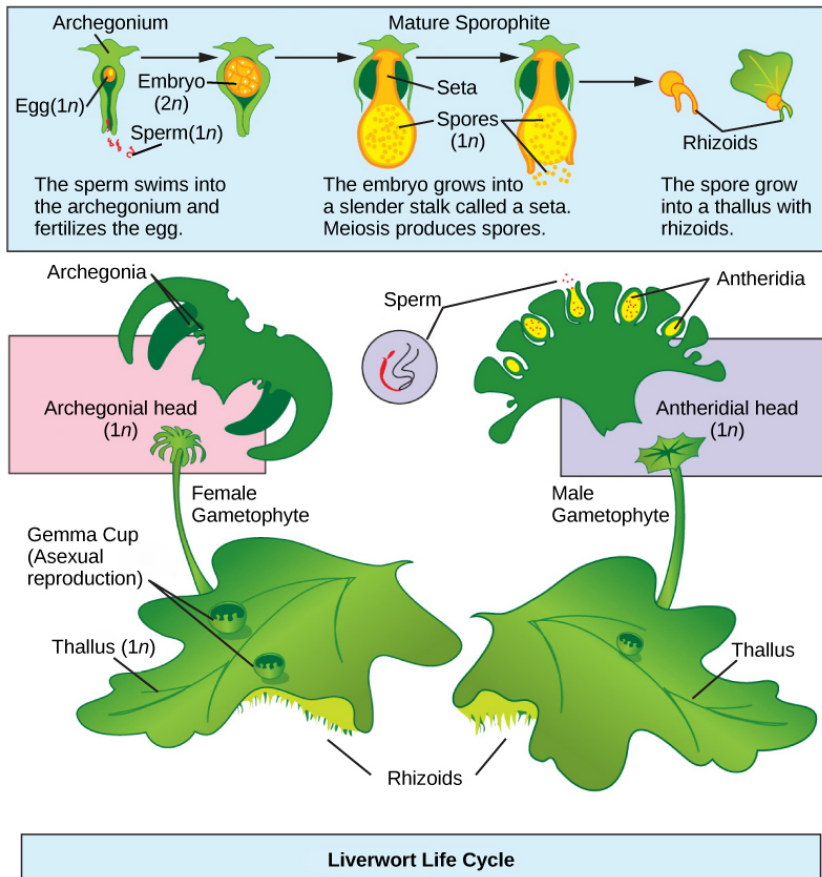
The life cycle of a typical liverwort is shown. (credit: modification of work by Mariana Ruiz Villareal)

Hornworts

The **hornworts** (*Anthocerotophyta*) belong to the broad bryophyte group. They have colonized a variety of habitats on land, although they are never far from a source of moisture. The short, blue-green gametophyte is the dominant phase of the lifecycle of a hornwort. The narrow, pipe-like

sporophyte is the defining characteristic of the group. The sporophytes emerge from the parent gametophyte and continue to grow throughout the life of the plant ([link]).

Hornworts grow a tall and slender sporophyte. (credit: modification of work by Jason Hollinger)

Stomata appear in the hornworts and are abundant on the sporophyte. Photosynthetic cells in the thallus contain a single chloroplast. Meristem cells at the base of the plant keep dividing and adding to its height. Many hornworts establish symbiotic relationships with cyanobacteria that fix nitrogen from the environment.

The lifecycle of hornworts ([link]) follows the general pattern of alternation of generations. The gametophytes grow as flat thalli on the soil with embedded gametangia. Flagellated sperm swim to the archegonia and fertilize eggs. The zygote develops into a long and slender sporophyte that eventually splits open, releasing spores. Thin cells called pseudoelaters surround the spores and help propel them further in the environment. Unlike the elaters observed in horsetails, the hornwort pseudoelaters are

single-celled structures. The haploid spores germinate and give rise to the next generation of gametophyte.
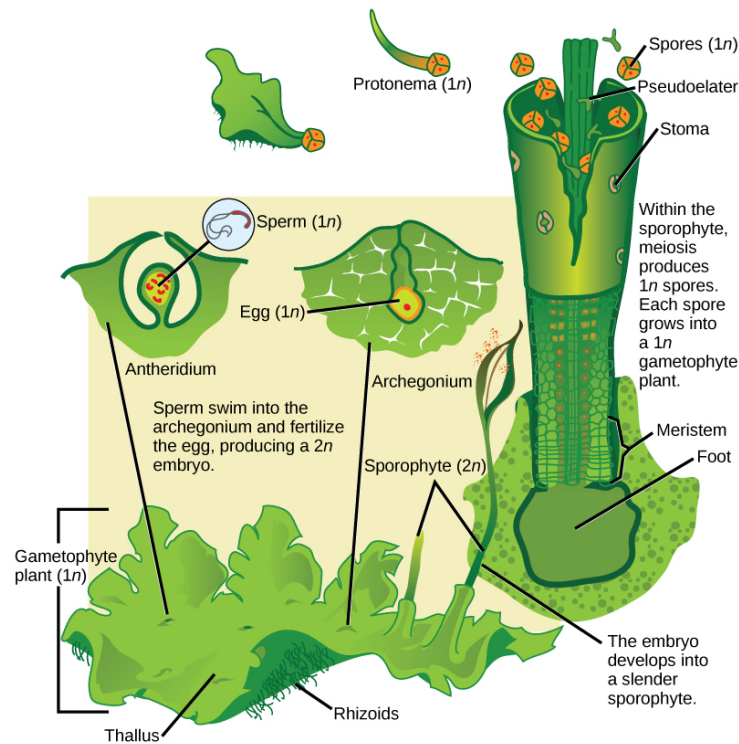
The alternation of generation in hornworts is shown. (credit: modification of work by "Smith609"/Wikimedia Commons based on original work by Mariana Ruiz Villareal)

Mosses

More than 10,000 species of **mosses** have been catalogued. Their habitats vary from the tundra, where they are the main vegetation, to the understory of tropical forests. In the tundra, the mosses' shallow rhizoids allow them to fasten to a substrate without penetrating the frozen soil. Mosses slow down

erosion, store moisture and soil nutrients, and provide shelter for small animals as well as food for larger herbivores, such as the musk ox. Mosses are very sensitive to air pollution and are used to monitor air quality. They are also sensitive to copper salts, so these salts are a common ingredient of compounds marketed to eliminate mosses from lawns.

Mosses form diminutive gametophytes, which are the dominant phase of the lifecycle. Green, flat structures—resembling true leaves, but lacking vascular tissue—are attached in a spiral to a central stalk. The plants absorb water and nutrients directly through these leaf-like structures. Some mosses have small branches. Some primitive traits of green algae, such as flagellated sperm, are still present in mosses that are dependent on water for reproduction. Other features of mosses are clearly adaptations to dry land. For example, stomata are present on the stems of the sporophyte, and a primitive vascular system runs up the sporophyte's stalk. Additionally, mosses are anchored to the substrate—whether it is soil, rock, or roof tiles—by multicellular **rhizoids**. These structures are precursors of roots. They originate from the base of the gametophyte, but are not the major route for the absorption of water and minerals. The lack of a true root system explains why it is so easy to rip moss mats from a tree trunk. The moss lifecycle follows the pattern of alternation of generations as shown in [link]. The most familiar structure is the haploid gametophyte, which germinates from a haploid spore and forms first a **protonema**—usually, a tangle of single-celled filaments that hug the ground. Cells akin to an apical meristem actively divide and give rise to a gametophore, consisting of a photosynthetic stem and foliage-like structures. Rhizoids form at the base of the gametophore. Gametangia of both sexes develop on separate gametophores. The male organ (the antheridium) produces many sperm, whereas the archegonium (the female organ) forms a single egg. At fertilization, the sperm swims down the neck to the venter and unites with the egg inside the archegonium. The zygote, protected by the archegonium, divides and grows into a sporophyte, still attached by its foot to the gametophyte.

Note:

Art Connection

Life Cycle of a Typical Moss
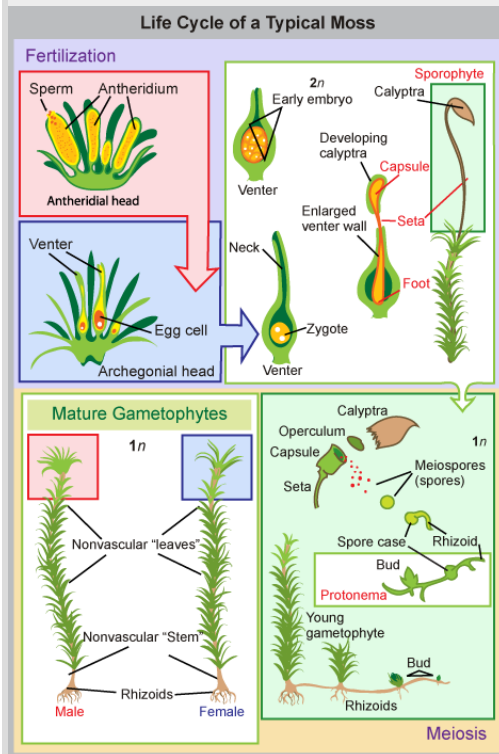
This illustration shows the life cycle of mosses. (credit: modification of work by Mariana Ruiz Villareal)

Which of the following statements about the moss life cycle is false?

a. The mature gametophyte is haploid.
b. The sporophyte produces haploid spores.
c. The calyptra buds to form a mature gametophyte.
d. The zygote is housed in the venter.

The slender **seta** (plural, setae), as seen in [link], contains tubular cells that transfer nutrients from the base of the sporophyte (the foot) to the

sporangium or **capsule**.

This photograph shows the long slender stems, called setae, connected to capsules of the moss *Thamnobryum alopecurum*. (credit: modification of work by Hermann Schachner)

A structure called a **peristome** increases the spread of spores after the tip of the capsule falls off at dispersal. The concentric tissue around the mouth of the capsule is made of triangular, close-fitting units, a little like "teeth"; these open and close depending on moisture levels, and periodically release spores.

Section Summary

Seedless nonvascular plants are small, having the gametophyte as the dominant stage of the lifecycle. Without a vascular system and roots, they absorb water and nutrients on all their exposed surfaces. Collectively known as bryophytes, the three main groups include the liverworts, the hornworts, and the mosses. Liverworts are the most primitive plants and are

closely related to the first land plants. Hornworts developed stomata and possess a single chloroplast per cell. Mosses have simple conductive cells and are attached to the substrate by rhizoids. They colonize harsh habitats and can regain moisture after drying out. The moss sporangium is a complex structure that allows release of spores away from the parent plant.

Art Connections

Exercise:

Problem:

[link] Which of the following statements about the moss life cycle is false?

- a. The mature gametophyte is haploid.
- b. The sporophyte produces haploid spores.
- c. The rhizoid buds to form a mature gametophyte.
- d. The zygote is housed in the venter.

Solution:

[link] C.

Review Questions

Exercise:

Problem:

Which of the following structures is not found in bryophytes?

- a. a cellulose cell wall
- b. chloroplast
- c. sporangium
- d. root

Solution:

D

Exercise:

Problem: Stomata appear in which group of plants?

    a. Charales
    b. liverworts
    c. hornworts
    d. mosses

Solution:

C

Exercise:

Problem: The chromosome complement in a moss protonema is:

    a. $1n$
    b. $2n$
    c. $3n$
    d. varies with the size of the protonema

Solution:

A

Exercise:

Problem: Why do mosses grow well in the Arctic tundra?

    a. They grow better at cold temperatures.
    b. They do not require moisture.

c. They do not have true roots and can grow on hard surfaces.
d. There are no herbivores in the tundra.

Solution:

C

Free Response

Exercise:

Problem:

In areas where it rains often, mosses grow on roofs. How do mosses survive on roofs without soil?

Solution:

Mosses absorb water and nutrients carried by the rain and do not need soil because they do not derive much nutrition from the soil.

Exercise:

Problem: What are the three classes of bryophytes?

Solution:

The bryophytes are divided into three phyla: the liverworts or Hepaticophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

Glossary

capsule
    case of the sporangium in mosses

gemma
> (plural, gemmae) leaf fragment that spreads for asexual reproduction

hornworts
> group of non-vascular plants in which stomata appear

liverworts
> most primitive group of the non-vascular plants

mosses
> group of bryophytes in which a primitive conductive system appears

peristome
> tissue that surrounds the opening of the capsule and allows periodic release of spores

protonema
> tangle of single celled filaments that forms from the haploid spore

rhizoids
> thin filaments that anchor the plant to the substrate

seta
> stalk that supports the capsule in mosses

Seedless Vascular Plants
By the end of this section, you will be able to:

- Identify the new traits that first appear in tracheophytes
- Discuss the importance of adaptations to life on land
- Describe the classes of seedless tracheophytes
- Describe the lifecycle of a fern
- Explain the role of seedless vascular plants in the ecosystem

The vascular plants, or **tracheophytes**, are the dominant and most conspicuous group of land plants. More than 260,000 species of tracheophytes represent more than 90 percent of Earth's vegetation. Several evolutionary innovations explain their success and their ability to spread to all habitats.

Bryophytes may have been successful at the transition from an aquatic habitat to land, but they are still dependent on water for reproduction, and absorb moisture and nutrients through the gametophyte surface. The lack of roots for absorbing water and minerals from the soil, as well as a lack of reinforced conducting cells, limits bryophytes to small sizes. Although they may survive in reasonably dry conditions, they cannot reproduce and expand their habitat range in the absence of water. Vascular plants, on the other hand, can achieve enormous heights, thus competing successfully for light. Photosynthetic organs become leaves, and pipe-like cells or vascular tissues transport water, minerals, and fixed carbon throughout the organism.

In seedless vascular plants, the diploid sporophyte is the dominant phase of the lifecycle. The gametophyte is now an inconspicuous, but still independent, organism. Throughout plant evolution, there is an evident reversal of roles in the dominant phase of the lifecycle. Seedless vascular plants still depend on water during fertilization, as the sperm must swim on a layer of moisture to reach the egg. This step in reproduction explains why ferns and their relatives are more abundant in damp environments.

Vascular Tissue: Xylem and Phloem

The first fossils that show the presence of vascular tissue date to the Silurian period, about 430 million years ago. The simplest arrangement of conductive cells shows a pattern of xylem at the center surrounded by phloem. **Xylem** is the tissue responsible for the storage and long-distance transport of water and nutrients, as well as the transfer of water-soluble growth factors from the organs of synthesis to the target organs. The tissue consists of conducting cells, known as tracheids, and supportive filler tissue, called parenchyma. Xylem conductive cells incorporate the compound **lignin** into their walls, and are thus described as lignified. Lignin itself is a complex polymer that is impermeable to water and confers mechanical strength to vascular tissue. With their rigid cell walls, the xylem cells provide support to the plant and allow it to achieve impressive heights. Tall plants have a selective advantage by being able to reach unfiltered sunlight and disperse their spores or seeds further away, thus expanding their range. By growing higher than other plants, tall trees cast their shadow on shorter plants and limit competition for water and precious nutrients in the soil.

Phloem is the second type of vascular tissue; it transports sugars, proteins, and other solutes throughout the plant. Phloem cells are divided into sieve elements (conducting cells) and cells that support the sieve elements. Together, xylem and phloem tissues form the vascular system of plants.

Roots: Support for the Plant

Roots are not well preserved in the fossil record. Nevertheless, it seems that roots appeared later in evolution than vascular tissue. The development of an extensive network of roots represented a significant new feature of vascular plants. Thin rhizoids attached bryophytes to the substrate, but these rather flimsy filaments did not provide a strong anchor for the plant; neither did they absorb substantial amounts of water and nutrients. In contrast, roots, with their prominent vascular tissue system, transfer water and minerals from the soil to the rest of the plant. The extensive network of roots that penetrates deep into the soil to reach sources of water also stabilizes trees by acting as a ballast or anchor. The majority of roots establish a symbiotic relationship with fungi, forming mycorrhizae, which

benefit the plant by greatly increasing the surface area for absorption of water and soil minerals and nutrients.

Leaves, Sporophylls, and Strobili

A third innovation marks the seedless vascular plants. Accompanying the prominence of the sporophyte and the development of vascular tissue, the appearance of true leaves improved their photosynthetic efficiency. Leaves capture more sunlight with their increased surface area by employing more chloroplasts to trap light energy and convert it to chemical energy, which is then used to fix atmospheric carbon dioxide into carbohydrates. The carbohydrates are exported to the rest of the plant by the conductive cells of phloem tissue.

The existence of two types of morphology suggests that leaves evolved independently in several groups of plants. The first type of leaf is the **microphyll**, or "little leaf," which can be dated to 350 million years ago in the late Silurian. A microphyll is small and has a simple vascular system. A single unbranched **vein**—a bundle of vascular tissue made of xylem and phloem—runs through the center of the leaf. Microphylls may have originated from the flattening of lateral branches, or from sporangia that lost their reproductive capabilities. Microphylls are present in the club mosses and probably preceded the development of **megaphylls**, or "big leaves", which are larger leaves with a pattern of branching veins. Megaphylls most likely appeared independently several times during the course of evolution. Their complex networks of veins suggest that several branches may have combined into a flattened organ, with the gaps between the branches being filled with photosynthetic tissue.

In addition to photosynthesis, leaves play another role in the life of the plants. Pine cones, mature fronds of ferns, and flowers are all **sporophylls** —leaves that were modified structurally to bear sporangia. **Strobili** are cone-like structures that contain sporangia. They are prominent in conifers and are commonly known as pine cones.

Ferns and Other Seedless Vascular Plants

By the late Devonian period, plants had evolved vascular tissue, well-defined leaves, and root systems. With these advantages, plants increased in height and size. During the Carboniferous period, swamp forests of club mosses and horsetails—some specimens reaching heights of more than 30 m (100 ft)—covered most of the land. These forests gave rise to the extensive coal deposits that gave the Carboniferous its name. In seedless vascular plants, the sporophyte became the dominant phase of the lifecycle.

Water is still required for fertilization of seedless vascular plants, and most favor a moist environment. Modern-day seedless tracheophytes include club mosses, horsetails, ferns, and whisk ferns.

Phylum Lycopodiophyta: Club Mosses

The **club mosses**, or phylum **Lycopodiophyta**, are the earliest group of seedless vascular plants. They dominated the landscape of the Carboniferous, growing into tall trees and forming large swamp forests. Today's club mosses are diminutive, evergreen plants consisting of a stem (which may be branched) and microphylls ([link]). The phylum Lycopodiophyta consists of close to 1,200 species, including the quillworts (*Isoetales*), the club mosses (*Lycopodiales*), and spike mosses (*Selaginellales*), none of which are true mosses or bryophytes.

Lycophytes follow the pattern of alternation of generations seen in the bryophytes, except that the sporophyte is the major stage of the lifecycle. The gametophytes do not depend on the sporophyte for nutrients. Some gametophytes develop underground and form mycorrhizal associations with fungi. In club mosses, the sporophyte gives rise to sporophylls arranged in strobili, cone-like structures that give the class its name. Lycophytes can be homosporous or heterosporous.

In the club mosses such as *Lycopodium clavatum*, sporangia are arranged in clusters called strobili. (credit: Cory Zanker)

Phylum Monilophyta: Class Equisetopsida (Horsetails)

Horsetails, whisk ferns and ferns belong to the phylum Monilophyta, with **horsetails** placed in the Class Equisetopsida. The single genus *Equisetum* is the survivor of a large group of plants, known as Arthrophyta, which produced large trees and entire swamp forests in the Carboniferous. The plants are usually found in damp environments and marshes ([link]).

Horsetails thrive in a marsh.
(credit: Myriam Feldman)

The stem of a horsetail is characterized by the presence of joints or nodes, hence the name Arthrophyta (arthro- = "joint"; -phyta = "plant"). Leaves and branches come out as whorls from the evenly spaced joints. The needle-shaped leaves do not contribute greatly to photosynthesis, the majority of which takes place in the green stem ([link]).

Thin leaves originating at the joints are noticeable on the horsetail plant. Horsetails were once used as scrubbing brushes and were nicknamed scouring brushes. (credit: Myriam Feldman)

Silica collects in the epidermal cells, contributing to the stiffness of horsetail plants. Underground stems known as rhizomes anchor the plants to the ground. Modern-day horsetails are homosporous and produce bisexual gametophytes.

Phylum Monilophyta: Class Psilotopsida (Whisk Ferns)

While most ferns form large leaves and branching roots, the **whisk ferns**, Class Psilotopsida, lack both roots and leaves, probably lost by reduction.

Photosynthesis takes place in their green stems, and small yellow knobs form at the tip of the branch stem and contain the sporangia. Whisk ferns were considered an early pterophytes. However, recent comparative DNA analysis suggests that this group may have lost both vascular tissue and roots through evolution, and is more closely related to ferns.

The whisk fern *Psilotum nudum* has conspicuous green stems with knob-shaped sporangia. (credit: Forest & Kim Starr)

Phylum Monilophyta: Class Psilotopsida (Ferns)

With their large fronds, **ferns** are the most readily recognizable seedless vascular plants. They are considered the most advanced seedless vascular plants and display characteristics commonly observed in seed plants. More than 20,000 species of ferns live in environments ranging from tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist, shaded places. Ferns made their appearance in the fossil record during the Devonian period and expanded during the Carboniferous.

The dominant stage of the lifecycle of a fern is the sporophyte, which consists of large compound leaves called fronds. Fronds fulfill a double role; they are photosynthetic organs that also carry reproductive organs. The stem may be buried underground as a rhizome, from which adventitious roots grow to absorb water and nutrients from the soil; or, they may grow above ground as a trunk in tree ferns ([link]). **Adventitious** organs are those that grow in unusual places, such as roots growing from the side of a stem.

Some specimens of this short tree-fern species can grow very tall. (credit: Adrian Pingstone)

The tip of a developing fern frond is rolled into a crozier, or fiddlehead ([link]**a** and [link]**b**). Fiddleheads unroll as the frond develops.

Croziers, or fiddleheads, are the tips of fern fronds. (credit a: modification of work by Cory Zanker; credit b: modification of work by Myriam Feldman)

The lifecycle of a fern is depicted in [link].
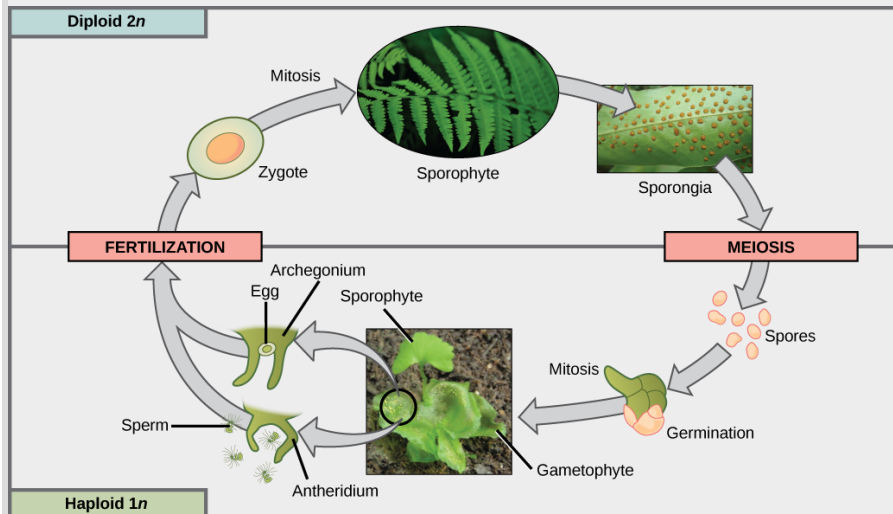
This life cycle of a fern shows alternation of generations with a dominant sporophyte stage. (credit "fern": modification of work by Cory Zanker; credit "gametophyte": modification of work by "Vlmastra"/Wikimedia Commons)

Which of the following statements about the fern life cycle is false?

a. Sporangia produce haploid spores.
b. The sporophyte grows from a gametophyte.

c. The sporophyte is diploid and the gametophyte is haploid.

d. Sporangia form on the underside of the gametophyte.

Most ferns produce the same type of spores and are therefore homosporous. The diploid sporophyte is the most conspicuous stage of the lifecycle. On the underside of its mature fronds, sori (singular, sorus) form as small clusters where sporangia develop ([link]).

Sori appear as small bumps on the underside of a fern frond. (credit:

Inside the sori, spores are produced by meiosis and released into the air. Those that land on a suitable substrate germinate and form a heart-shaped gametophyte, which is attached to the ground by thin filamentous rhizoids ([link]).
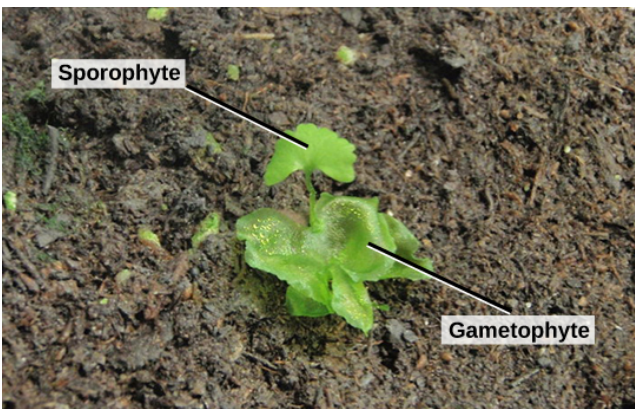
Shown here are a young sporophyte (upper part of image) and a heart-shaped gametophyte (bottom part of image). (credit: modification of work by "Vlmastra"/Wikimedia Commons)

The inconspicuous gametophyte harbors both sex gametangia. Flagellated sperm released from the antheridium swim on a wet surface to the archegonium, where the egg is fertilized. The newly formed zygote grows into a sporophyte that emerges from the gametophyte and grows by mitosis into the next generation sporophyte.

Landscape Designer

Looking at the well-laid parterres of flowers and fountains in the grounds of royal castles and historic houses of Europe, it's clear that the gardens' creators knew about more than art and design. They were also familiar with the biology of the plants they chose. Landscape design also has strong roots in the United States' tradition. A prime example of early American classical design is Monticello: Thomas Jefferson's private estate. Among his many interests, Jefferson maintained a strong passion for botany. Landscape layout can encompass a small private space, like a backyard garden; public gathering places, like Central Park in New York City; or an entire city plan, like Pierre L'Enfant's design for Washington, DC.

A landscape designer will plan traditional public spaces—such as botanical gardens, parks, college campuses, gardens, and larger developments—as well as natural areas and private gardens. The restoration of natural places encroached on by human intervention, such as wetlands, also requires the expertise of a landscape designer.

With such an array of necessary skills, a landscape designer's education includes a solid background in botany, soil science, plant pathology, entomology, and horticulture. Coursework in architecture and design software is also required for the completion of the degree. The successful design of a landscape rests on an extensive knowledge of plant growth requirements, such as light and shade, moisture levels, compatibility of different species, and susceptibility to pathogens and pests. Mosses and ferns will thrive in a shaded area, where fountains provide moisture; cacti, on the other hand, would not fare well in that environment. The future growth of individual plants must be taken into account, to avoid crowding and competition for light and nutrients. The appearance of the space over time is also of concern. Shapes, colors, and biology must be balanced for a well-maintained and sustainable green space. Art, architecture, and biology blend in a beautifully designed and implemented landscape.

This landscaped border at a college campus was designed by students in the horticulture and landscaping department of the college. (credit: Myriam Feldman)

The Importance of Seedless Vascular Plants

Mosses and liverworts are often the first macroscopic organisms to colonize an area, both in a primary succession—where bare land is settled for the first time by living organisms—or in a secondary succession, where soil remains intact after a catastrophic event wipes out many existing species. Their spores are carried by the wind, birds, or insects. Once mosses and liverworts are established, they provide food and shelter for other species. In a hostile environment, like the tundra where the soil is frozen, bryophytes grow well because they do not have roots and can dry and rehydrate rapidly once water is again available. Mosses are at the base of the food chain in the tundra biome. Many species—from small insects to musk oxen and reindeer—depend on mosses for food. In turn, predators feed on the herbivores, which are the primary consumers. Some reports indicate that bryophytes make the soil more amenable to colonization by other plants. Because they establish symbiotic relationships with nitrogen-fixing cyanobacteria, mosses replenish the soil with nitrogen.

At the end of the nineteenth century, scientists observed that lichens and mosses were becoming increasingly rare in urban and suburban areas. Since bryophytes have neither a root system for absorption of water and nutrients, nor a cuticle layer that protects them from desiccation, pollutants in rainwater readily penetrate their tissues; they absorb moisture and nutrients through their entire exposed surfaces. Therefore, pollutants dissolved in rainwater penetrate plant tissues readily and have a larger impact on mosses than on other plants. The disappearance of mosses can be considered a bioindicator for the level of pollution in the environment.

Ferns contribute to the environment by promoting the weathering of rock, accelerating the formation of topsoil, and slowing down erosion by spreading rhizomes in the soil. The water ferns of the genus *Azolla* harbor nitrogen-fixing cyanobacteria and restore this important nutrient to aquatic habitats.

Seedless plants have historically played a role in human life through uses as tools, fuel, and medicine. Dried **peat moss**, *Sphagnum*, is commonly used as fuel in some parts of Europe and is considered a renewable resource. *Sphagnum* bogs ([link]) are cultivated with cranberry and blueberry bushes. The ability of *Sphagnum* to hold moisture makes the moss a common soil conditioner. Florists use blocks of *Sphagnum* to maintain moisture for floral arrangements.

Sphagnum acutifolium is dried peat moss and can be used as

fuel. (credit: Ken Goulding)

The attractive fronds of ferns make them a favorite ornamental plant. Because they thrive in low light, they are well suited as house plants. More importantly, fiddleheads are a traditional spring food of Native Americans in the Pacific Northwest, and are popular as a side dish in French cuisine. The licorice fern, *Polypodium glycyrrhiza,* is part of the diet of the Pacific Northwest coastal tribes, owing in part to the sweetness of its rhizomes. It has a faint licorice taste and serves as a sweetener. The rhizome also figures in the pharmacopeia of Native Americans for its medicinal properties and is used as a remedy for sore throat.

Note:
LInk to Learning

Go to this website to learn how to identify fern species based upon their fiddleheads.

By far the greatest impact of seedless vascular plants on human life, however, comes from their extinct progenitors. The tall club mosses, horsetails, and tree-like ferns that flourished in the swampy forests of the Carboniferous period gave rise to large deposits of coal throughout the world. Coal provided an abundant source of energy during the Industrial Revolution, which had tremendous consequences on human societies, including rapid technological progress and growth of large cities, as well as

the degradation of the environment. Coal is still a prime source of energy and also a major contributor to global warming.

Section Summary

Vascular systems consist of xylem tissue, which transports water and minerals, and phloem tissue, which transports sugars and proteins. With the development of the vascular system, there appeared leaves to act as large photosynthetic organs, and roots to access water from the ground. Small uncomplicated leaves are microphylls. Large leaves with vein patterns are megaphylls. Modified leaves that bear sporangia are sporophylls. Some sporophylls are arranged in cone structures called strobili.

The seedless vascular plants include club mosses, which are the most primitive; whisk ferns, which lost leaves and roots by reductive evolution; and horsetails and ferns. Ferns are the most advanced group of seedless vascular plants. They are distinguished by large leaves called fronds and small sporangia-containing structures called sori, which are found on the underside of the fronds.

Mosses play an essential role in the balance of the ecosystems; they are pioneering species that colonize bare or devastated environments and make it possible for a succession to occur. They contribute to the enrichment of the soil and provide shelter and nutrients for animals in hostile environments. Mosses and ferns can be used as fuels and serve culinary, medical, and decorative purposes.

Art Connections

Exercise:

  Problem:

  [link] Which of the following statements about the fern life cycle is false?

      a. Sporangia produce haploid spores.

b. The sporophyte grows from a gametophyte.
c. The sporophyte is diploid and the gametophyte is haploid.
d. Sporangia form on the underside of the gametophyte.

Solution:

[link] D.

Review Questions

Exercise:

Problem: Microphylls are characteristic of which types of plants?

a. mosses
b. liverworts
c. club mosses
d. ferns

Solution:

C

Exercise:

Problem:

A plant in the understory of a forest displays a segmented stem and slender leaves arranged in a whorl. It is probably a _____.

a. club moss
b. whisk fern
c. fern
d. horsetail

Solution:

D

Exercise:

Problem:

The following structures are found on the underside of fern leaves and contain sporangia:

 a. sori
 b. rhizomes
 c. megaphylls
 d. microphylls

Solution:

A

Exercise:

Problem: The dominant organism in fern is the _____.

 a. sperm
 b. spore
 c. gamete
 d. sporophyte

Solution:

D

Exercise:

Problem: What seedless plant is a renewable source of energy?

a. club moss
b. horsetail
c. sphagnum moss
d. fern

Solution:

C

Exercise:

Problem: How do mosses contribute to returning nitrogen to the soil?

a. Mosses fix nitrogen from the air.
b. Mosses harbor cyanobacteria that fix nitrogen.
c. Mosses die and return nitrogen to the soil.
d. Mosses decompose rocks and release nitrogen.

Solution:

D

Free Response

Exercise:

Problem:

How did the development of a vascular system contribute to the increase in size of plants?

Solution:

Plants became able to transport water and nutrients and not be limited by rates of diffusion. Vascularization allowed the development of

leaves, which increased efficiency of photosynthesis and provided more energy for plant growth.

Exercise:

Problem:

Which plant is considered the most advanced seedless vascular plant and why?

Solution:

Ferns are considered the most advanced seedless vascular plants, because they display characteristics commonly observed in seed plants —they form large leaves and branching roots.

Glossary

adventitious
    describes an organ that grows in an unusual place, such as a roots growing from the side of a stem

club mosses
    earliest group of seedless vascular plants

fern
    seedless vascular plant that produces large fronds; the most advanced group of seedless vascular plants

horsetail
    seedless vascular plant characterized by joints

lignin
    complex polymer impermeable to water

lycophyte
    club moss

megaphyll
    larger leaves with a pattern of branching veins

microphyll
    small size and simple vascular system with a single unbranched vein

peat moss
    Sphagnum

phloem
    tissue responsible for transport of sugars, proteins, and other solutes

sporophyll
    leaf modified structurally to bear sporangia

strobili
    cone-like structures that contain the sporangia

tracheophyte
    vascular plant

vein
    bundle of vascular tissue made of xylem and phloem

whisk fern
    seedless vascular plant that lost roots and leaves by reduction

xylem
    tissue responsible for long-distance transport of water and nutrients

Introduction
class="introduction"

Seed plants dominate the landscape and play an integral role in human societies. (a) Palm trees grow along the shoreline; (b) wheat is a crop grown in most of the world; (c) the flower of the cotton plant produces fibers that are woven into fabric; (d) the potent alkaloids of the beautiful opium poppy have influenced human life both as a medicinal

remedy and as a dangerously addictive drug. (credit a: modification of work by Ryan Kozie; credit b: modification of work by Stephen Ausmus; credit c: modification of work by David Nance; credit d: modification of work by Jolly Janner)

(a)   (b)   (c)   (d)

The lush palms on tropical shorelines do not depend on water for the dispersal of their pollen, fertilization, or the survival of the zygote—unlike mosses, liverworts, and ferns of the terrain. Seed plants, such as palms, have broken free from the need to rely on water for their reproductive needs. They play an integral role in all aspects of life on the planet, shaping the physical terrain, influencing the climate, and maintaining life as we know it. For millennia, human societies have depended on seed plants for nutrition and medicinal compounds: and more recently, for industrial by-products, such as timber and paper, dyes, and textiles. Palms provide materials including rattans, oils, and dates. Wheat is grown to feed both human and animal populations. The fruit of the cotton boll flower is harvested as a boll, with its fibers transformed into clothing or pulp for paper. The showy opium poppy is valued both as an ornamental flower and as a source of potent opiate compounds.

Evolution of Seed Plants
By the end of this section, you will be able to:

- Explain when seed plants first appeared and when gymnosperms became the dominant plant group
- Describe the two major innovations that allowed seed plants to reproduce in the absence of water
- Discuss the purpose of pollen grains and seeds
- Describe the significance of angiosperms bearing both flowers and fruit

The first plants to colonize land were most likely closely related to modern day mosses (bryophytes) and are thought to have appeared about 500 million years ago. They were followed by liverworts (also bryophytes) and primitive vascular plants—the pterophytes—from which modern ferns are derived. The lifecycle of bryophytes and pterophytes is characterized by the alternation of generations, like gymnosperms and angiosperms; what sets bryophytes and pterophytes apart from gymnosperms and angiosperms is their reproductive requirement for water. The completion of the bryophyte and pterophyte life cycle requires water because the male gametophyte releases sperm, which must swim—propelled by their flagella—to reach and fertilize the female gamete or egg. After fertilization, the zygote matures and grows into a sporophyte, which in turn will form sporangia or "spore vessels." In the sporangia, mother cells undergo meiosis and produce the haploid spores. Release of spores in a suitable environment will lead to germination and a new generation of gametophytes.

In seed plants, the evolutionary trend led to a dominant sporophyte generation, and at the same time, a systematic reduction in the size of the gametophyte: from a conspicuous structure to a microscopic cluster of cells enclosed in the tissues of the sporophyte. Whereas lower vascular plants, such as club mosses and ferns, are mostly homosporous (produce only one type of spore), all seed plants, or **spermatophytes**, are heterosporous. They form two types of spores: megaspores (female) and microspores (male). Megaspores develop into female gametophytes that produce eggs, and microspores mature into male gametophytes that generate sperm. Because the gametophytes mature within the spores, they are not free-living, as are

the gametophytes of other seedless vascular plants. Heterosporous seedless plants are seen as the evolutionary forerunners of seed plants.

Seeds and pollen—two critical adaptations to drought, and to reproduction that doesn't require water—distinguish seed plants from other (seedless) vascular plants. Both adaptations were required for the colonization of land begun by the bryophytes and their ancestors. Fossils place the earliest distinct seed plants at about 350 million years ago. The first reliable record of gymnosperms dates their appearance to the Pennsylvanian period, about 319 million years ago ([link]). Gymnosperms were preceded by **progymnosperms**, the first naked seed plants, which arose about 380 million years ago. Progymnosperms were a transitional group of plants that superficially resembled conifers (cone bearers) because they produced wood from the secondary growth of the vascular tissues; however, they still reproduced like ferns, releasing spores into the environment. Gymnosperms dominated the landscape in the early (Triassic) and middle (Jurassic) Mesozoic era. Angiosperms surpassed gymnosperms by the middle of the Cretaceous (about 100 million years ago) in the late Mesozoic era, and today are the most abundant plant group in most terrestrial biomes.

EON	ERA	PERIOD	MILLIONS OF YEARS AGO
Phanerozoic	Cenozoic	Quaternary	--- 1.6 --
		Tertiary	--- 66 --
	Mesozoic	Cretaceous	---138 --
		Jurassic	-- 205 --
		Triassic	-- 240 --
	Paleozoic	Permian	-- 290 --
		Pennsylvanian	---330 --
		Mississippian	-- 360 --
		Devonian	-- 410 --
		Silurian	-- 435 --
		Ordovician	-- 500 --
		Cambrian	-- 570 --
Proterozoic	Late Proterozoic Middle Proterozoic Early Proterozoic		--2500--
Archean	Late Archean Middle Archean Early Archean		-- 3800?--
Pre-Archean			

Various plant species evolved in different eras. (credit: United States

Geological Survey)

Pollen and seed were innovative structures that allowed seed plants to break their dependence on water for reproduction and development of the embryo, and to conquer dry land. The **pollen grains** are the male gametophytes, which contain the sperm (gametes) of the plant. The small haploid ($1n$) cells are encased in a protective coat that prevents desiccation (drying out) and mechanical damage. Pollen grains can travel far from their original sporophyte, spreading the plant's genes. The **seed** offers the embryo protection, nourishment, and a mechanism to maintain dormancy for tens or even thousands of years, ensuring germination can occur when growth conditions are optimal. Seeds therefore allow plants to disperse the next generation through both space and time. With such evolutionary advantages, seed plants have become the most successful and familiar group of plants, in part because of their size and striking appearance.

Evolution of Gymnosperms

The fossil plant *Elkinsia polymorpha*, a "seed fern" from the Devonian period—about 400 million years ago—is considered the earliest seed plant known to date. Seed ferns ([link]) produced their seeds along their branches without specialized structures. What makes them the first true seed plants is that they developed structures called cupules to enclose and protect the **ovule**—the female gametophyte and associated tissues—which develops into a seed upon fertilization. Seed plants resembling modern tree ferns became more numerous and diverse in the coal swamps of the Carboniferous period.

This fossilized leaf is from *Glossopteris*, a seed fern that thrived during the Permian age (290–240 million years ago). (credit: D.L. Schmidt, USGS)

Fossil records indicate the first gymnosperms (progymnosperms) most likely originated in the Paleozoic era, during the middle Devonian period: about 390 million years ago. Following the wet Mississippian and Pennsylvanian periods, which were dominated by giant fern trees, the Permian period was dry. This gave a reproductive edge to seed plants, which are better adapted to survive dry spells. The Ginkgoales, a group of gymnosperms with only one surviving species—the *Gingko biloba*—were the first gymnosperms to appear during the lower Jurassic. Gymnosperms expanded in the Mesozoic era (about 240 million years ago), supplanting ferns in the landscape, and reaching their greatest diversity during this time. The Jurassic period was as much the age of the cycads (palm-tree-like gymnosperms) as the age of the dinosaurs. Gingkoales and the more familiar conifers also dotted the landscape. Although angiosperms (flowering plants) are the major form of plant life in most biomes, gymnosperms still dominate some ecosystems, such as the taiga (boreal forests) and the alpine forests at higher mountain elevations ([link]) because of their adaptation to cold and dry growth conditions.

This boreal forest (taiga) has low-lying plants and conifer trees. (credit: L.B. Brubaker, NOAA)

Seeds and Pollen as an Evolutionary Adaptation to Dry Land

Unlike bryophyte and fern spores (which are haploid cells dependent on moisture for rapid development of gametophytes), seeds contain a diploid embryo that will germinate into a sporophyte. Storage tissue to sustain growth and a protective coat give seeds their superior evolutionary advantage. Several layers of hardened tissue prevent desiccation, and free reproduction from the need for a constant supply of water. Furthermore, seeds remain in a state of dormancy—induced by desiccation and the hormone abscisic acid—until conditions for growth become favorable. Whether blown by the wind, floating on water, or carried away by animals, seeds are scattered in an expanding geographic range, thus avoiding competition with the parent plant.

Pollen grains ([link]) are male gametophytes and are carried by wind, water, or a pollinator. The whole structure is protected from desiccation and can reach the female organs without dependence on water. Male gametes reach female gametophyte and the egg cell gamete though a pollen tube: an extension of a cell within the pollen grain. The sperm of modern

gymnosperms lack flagella, but in cycads and the *Gingko*, the sperm still possess flagella that allow them to swim down the **pollen tube** to the female gamete; however, they are enclosed in a pollen grain.
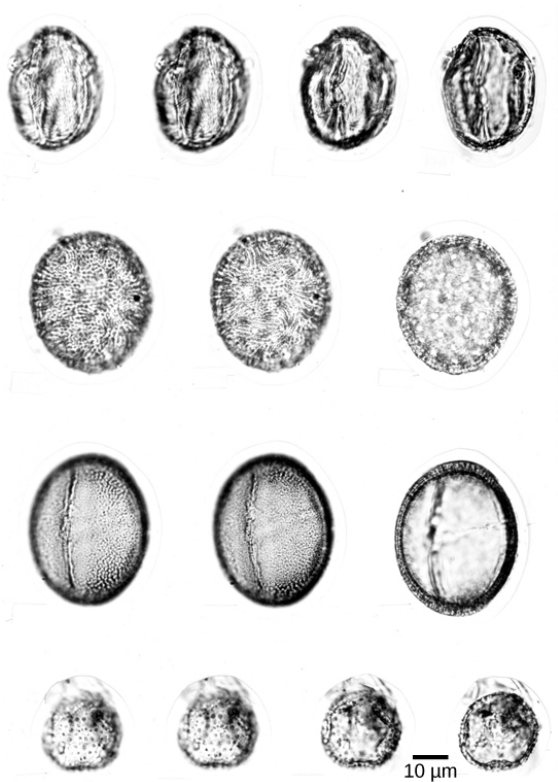
This fossilized pollen is from a Buckbean fen core found in Yellowstone National Park, Wyoming. The pollen is magnified 1,054 times. (credit: R.G. Baker, USGS; scale-bar data from Matt Russell)

Evolution of Angiosperms

Undisputed fossil records place the massive appearance and diversification of angiosperms in the middle to late Mesozoic era. Angiosperms ("seed in a vessel") produce a flower containing male and/or female reproductive structures. Fossil evidence ([link]) indicates that flowering plants first appeared in the Lower Cretaceous, about 125 million years ago, and were rapidly diversifying by the Middle Cretaceous, about 100 million years ago. Earlier traces of angiosperms are scarce. Fossilized pollen recovered from Jurassic geological material has been attributed to angiosperms. A few early Cretaceous rocks show clear imprints of leaves resembling angiosperm leaves. By the mid-Cretaceous, a staggering number of diverse flowering plants crowd the fossil record. The same geological period is also marked by the appearance of many modern groups of insects, including pollinating insects that played a key role in ecology and the evolution of flowering plants.

Although several hypotheses have been offered to explain this sudden profusion and variety of flowering plants, none have garnered the consensus of paleobotanists (scientists who study ancient plants). New data in comparative genomics and paleobotany have, however, shed some light on the evolution of angiosperms. Rather than being derived from gymnosperms, angiosperms form a sister clade (a species and its descendents) that developed in parallel with the gymnosperms. The two innovative structures of flowers and fruit represent an improved reproductive strategy that served to protect the embryo, while increasing genetic variability and range. Paleobotanists debate whether angiosperms evolved from small woody bushes, or were basal angiosperms related to tropical grasses. Both views draw support from cladistics studies, and the so-called woody magnoliid hypothesis—which proposes that the early ancestors of angiosperms were shrubs—also offers molecular biological evidence.

The most primitive living angiosperm is considered to be *Amborella trichopoda*, a small plant native to the rainforest of New Caledonia, an island in the South Pacific. Analysis of the genome of *A. trichopoda* has shown that it is related to all existing flowering plants and belongs to the oldest confirmed branch of the angiosperm family tree. A few other angiosperm groups called basal angiosperms, are viewed as primitive

because they branched off early from the phylogenetic tree. Most modern angiosperms are classified as either monocots or eudicots, based on the structure of their leaves and embryos. Basal angiosperms, such as water lilies, are considered more primitive because they share morphological traits with both monocots and eudicots.

This leaf imprint shows a *Ficus speciosissima*, an angiosperm that flourished during the Cretaceous period. (credit: W. T. Lee, USGS)

Flowers and Fruits as an Evolutionary Adaptation

Angiosperms produce their gametes in separate organs, which are usually housed in a **flower**. Both fertilization and embryo development take place inside an anatomical structure that provides a stable system of sexual reproduction largely sheltered from environmental fluctuations. Flowering plants are the most diverse phylum on Earth after insects; flowers come in a bewildering array of sizes, shapes, colors, smells, and arrangements. Most flowers have a mutualistic pollinator, with the distinctive features of flowers reflecting the nature of the pollination agent. The relationship between pollinator and flower characteristics is one of the great examples of coevolution.

Following fertilization of the egg, the ovule grows into a seed. The surrounding tissues of the ovary thicken, developing into a **fruit** that will protect the seed and often ensure its dispersal over a wide geographic range. Not all fruits develop from an ovary; such structures are "false fruits." Like flowers, fruit can vary tremendously in appearance, size, smell, and taste. Tomatoes, walnut shells and avocados are all examples of fruit. As with pollen and seeds, fruits also act as agents of dispersal. Some may be carried away by the wind. Many attract animals that will eat the fruit and pass the seeds through their digestive systems, then deposit the seeds in another location. Cockleburs are covered with stiff, hooked spines that can hook into fur (or clothing) and hitch a ride on an animal for long distances. The cockleburs that clung to the velvet trousers of an enterprising Swiss hiker, George de Mestral, inspired his invention of the loop and hook fastener he named Velcro.

Note:
Evolution Connection
Building Phylogenetic Trees with Analysis of DNA Sequence Alignments
All living organisms display patterns of relationships derived from their evolutionary history. Phylogeny is the science that describes the relative connections between organisms, in terms of ancestral and descendant species. Phylogenetic trees, such as the plant evolutionary history shown in [link], are tree-like branching diagrams that depict these relationships.

Species are found at the tips of the branches. Each branching point, called a node, is the point at which a single taxonomic group (taxon), such as a species, separates into two or more species.
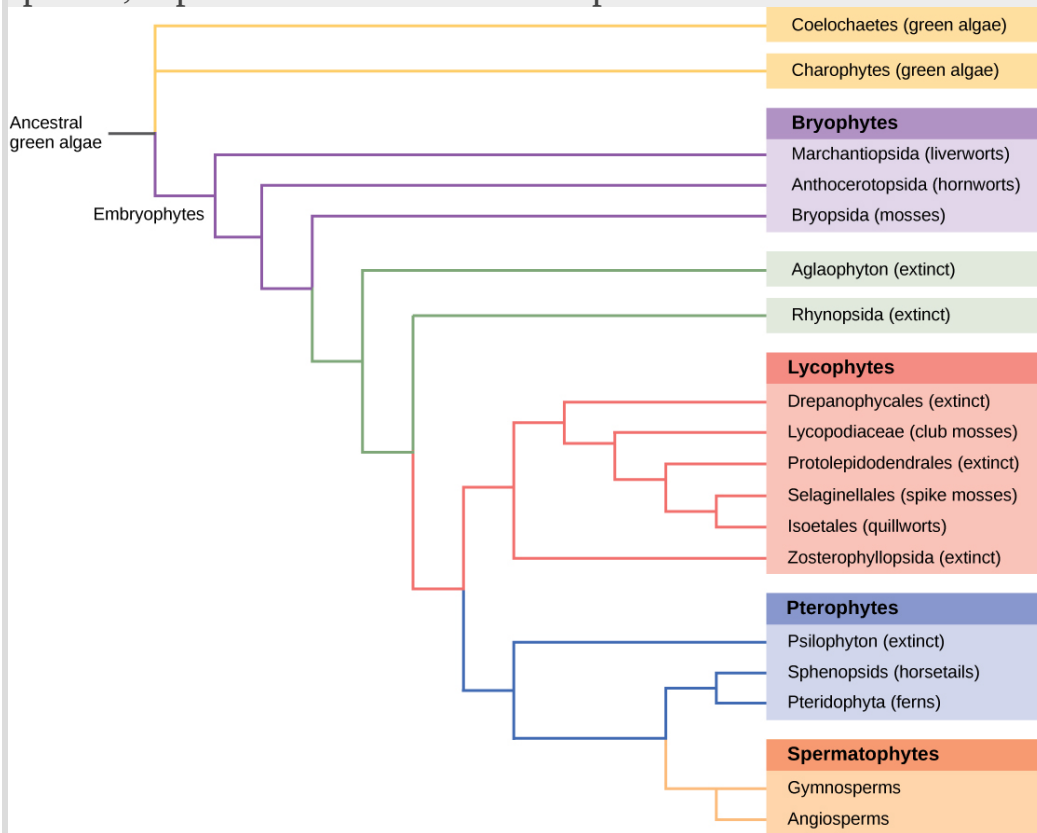
This phylogenetic tree shows the evolutionary relationships of plants.

Phylogenetic trees have been built to describe the relationships between species since Darwin's time. Traditional methods involve comparison of homologous anatomical structures and embryonic development, assuming that closely related organisms share anatomical features during embryo development. Some traits that disappear in the adult are present in the embryo; for example, a human fetus, at one point, has a tail. The study of fossil records shows the intermediate stages that link an ancestral form to its descendants. Most of these approaches are imprecise and lend themselves to multiple interpretations. As the tools of molecular biology and computational analysis have been developed and perfected in recent years, a new generation of tree-building methods has taken shape. The key

assumption is that genes for essential proteins or RNA structures, such as the ribosomal RNA, are inherently conserved because mutations (changes in the DNA sequence) could compromise the survival of the organism. DNA from minute amounts of living organisms or fossils can be amplified by polymerase chain reaction (PCR) and sequenced, targeting the regions of the genome that are most likely to be conserved between species. The genes encoding the ribosomal RNA from the small 18S subunit and plastid genes are frequently chosen for DNA alignment analysis.

Once the sequences of interest are obtained, they are compared with existing sequences in databases such as GenBank, which is maintained by The National Center for Biotechnology Information. A number of computational tools are available to align and analyze sequences. Sophisticated computer analysis programs determine the percentage of sequence identity or homology. Sequence homology can be used to estimate the evolutionary distance between two DNA sequences and reflect the time elapsed since the genes separated from a common ancestor. Molecular analysis has revolutionized phylogenetic trees. In some cases, prior results from morphological studies have been confirmed: for example, confirming *Amborella trichopoda* as the most primitive angiosperm known. However, some groups and relationships have been rearranged as a result of DNA analysis.

Section Summary

Seed plants appeared about one million years ago, during the Carboniferous period. Two major innovations—seed and pollen—allowed seed plants to reproduce in the absence of water. The gametophytes of seed plants shrank, while the sporophytes became prominent structures and the diploid stage became the longest phase of the lifecycle. Gymnosperms became the dominant group during the Triassic. In these, pollen grains and seeds protect against desiccation. The seed, unlike a spore, is a diploid embryo surrounded by storage tissue and protective layers. It is equipped to delay germination until growth conditions are optimal. Angiosperms bear both flowers and fruit. The structures protect the gametes and the embryo during

its development. Angiosperms appeared during the Mesozoic era and have become the dominant plant life in terrestrial habitats.

Review Questions

Exercise:

Problem: Seed plants are _____.

    a. all homosporous.
    b. mostly homosporous with some heterosporous.
    c. mostly heterosporous with some homosporous.
    d. all heterosporous.

Solution:

D

Exercise:

Problem:

Besides the seed, what other major structure diminishes a plant's reliance on water for reproduction?

    a. flower
    b. fruit
    c. pollen
    d. spore

Solution:

A

Exercise:

Problem:

In which of the following geological periods would gymnosperms dominate the landscape?

  a. Carboniferous
  b. Permian
  c. Triassic
  d. Eocene (present)

Solution:

  C

Exercise:

Problem:

Which of the following structures widens the geographic range of a species and is an agent of dispersal?

  a. seed
  b. flower
  c. leaf
  d. root

Solution:

  A

Free Response

Exercise:

Problem:

The Triassic Period was marked by the increase in number and variety of angiosperms. Insects also diversified enormously during the same period. Can you propose the reason or reasons that could foster coevolution?

Solution:

Both pollination and herbivory contributed to diversity, with plants needing to attract some insects and repel others.

Exercise:

Problem:

What role did the adaptations of seed and pollen play in the development and expansion of seed plants?

Solution:

Seeds and pollen allowed plants to reproduce in absence of water. This allowed them to expand their range onto dry land and to survive drought conditions.

Glossary

flower
    branches specialized for reproduction found in some seed-bearing plants, containing either specialized male or female organs or both male and female organs

fruit
    thickened tissue derived from ovary wall that protects the embryo after fertilization and facilitates seed dispersal

ovule
    female gametophyte

pollen grain
 structure containing the male gametophyte of the plant

pollen tube
 extension from the pollen grain that delivers sperm to the egg cell

progymnosperm
 transitional group of plants that resembled conifers because they
 produced wood, yet still reproduced like ferns

seed
 structure containing the embryo, storage tissue and protective coat

spermatophyte
 seed plant; from the Greek *sperm* (seed) and *phyte* (plant)

Gymnosperms
By the end of this section, you will be able to:

- Discuss the type of seeds produced by gymnosperms, as well as other characteristics of gymnosperms
- State which period saw the first appearance of gymnosperms and explain when they were the dominant plant life
- List the four groups of modern-day gymnosperms and provide examples of each

Gymnosperms, meaning "naked seeds," are a diverse group of seed plants and are paraphyletic. Paraphyletic groups are those in which not all members are descendants of a single common ancestor. Their characteristics include naked seeds, separate female and male gametes, pollination by wind, and tracheids (which transport water and solutes in the vascular system).

Gymnosperm seeds are not enclosed in an ovary; rather, they are exposed on cones or modified leaves. Sporophylls are specialized leaves that produce sporangia. The term **strobilus** (plural = strobili) describes a tight arrangement of sporophylls around a central stalk, as seen in cones. Some seeds are enveloped by sporophyte tissues upon maturation. The layer of sporophyte tissue that surrounds the megasporangium, and later, the embryo, is called the **integument**.

Gymnosperms were the dominant phylum in Mesozoic era. They are adapted to live where fresh water is scarce during part of the year, or in the nitrogen-poor soil of a bog. Therefore, they are still the prominent phylum in the coniferous biome or taiga, where the evergreen conifers have a selective advantage in cold and dry weather. Evergreen conifers continue low levels of photosynthesis during the cold months, and are ready to take advantage of the first sunny days of spring. One disadvantage is that conifers are more susceptible than deciduous trees to infestations because conifers do not lose their leaves all at once. They cannot, therefore, shed parasites and restart with a fresh supply of leaves in spring.

The life cycle of a gymnosperm involves alternation of generations, with a dominant sporophyte in which the female gametophyte resides, and reduced

gametophytes. All gymnosperms are heterosporous. The male and female reproductive organs can form in cones or strobili. Male and female sporangia are produced either on the same plant, described as **monoecious** ("one home" or bisexual), or on separate plants, referred to as **dioecious** ("two homes" or unisexual) plants. The life cycle of a conifer will serve as our example of reproduction in gymnosperms.

Life Cycle of a Conifer

Pine trees are conifers (cone bearing) and carry both male and female sporophylls on the same mature sporophyte. Therefore, they are monoecious plants. Like all gymnosperms, pines are heterosporous and generate two different types of spores: male microspores and female megaspores. In the male cones, or staminate cones, the **microsporocytes** give rise to pollen grains by meiosis. In the spring, large amounts of yellow pollen are released and carried by the wind. Some gametophytes will land on a female cone. Pollination is defined as the initiation of pollen tube growth. The pollen tube develops slowly, and the generative cell in the pollen grain divides into two haploid sperm cells by mitosis. At fertilization, one of the sperm cells will finally unite its haploid nucleus with the haploid nucleus of a haploid egg cell.

Female cones, or **ovulate cones**, contain two ovules per scale. One megaspore mother cell, or **megasporocyte**, undergoes meiosis in each ovule. Three of the four cells break down; only a single surviving cell will develop into a female multicellular gametophyte, which encloses archegonia (an archegonium is a reproductive organ that contains a single large egg). Upon fertilization, the diploid egg will give rise to the embryo, which is enclosed in a seed coat of tissue from the parent plant. Fertilization and seed development is a long process in pine trees: it may take up to two years after pollination. The seed that is formed contains three generations of tissues: the seed coat that originates from the sporophyte tissue, the gametophyte that will provide nutrients, and the embryo itself.

[link] illustrates the life cycle of a conifer. The sporophyte ($2n$) phase is the longest phase in the life of a gymnosperm. The gametophytes ($1n$)—microspores and megaspores—are reduced in size. It may take more than

year between pollination and fertilization while the pollen tube grows towards the megasporocyte (2n), which undergoes meiosis into megaspores. The megaspores will mature into eggs (1n).

Note:
Art Connection
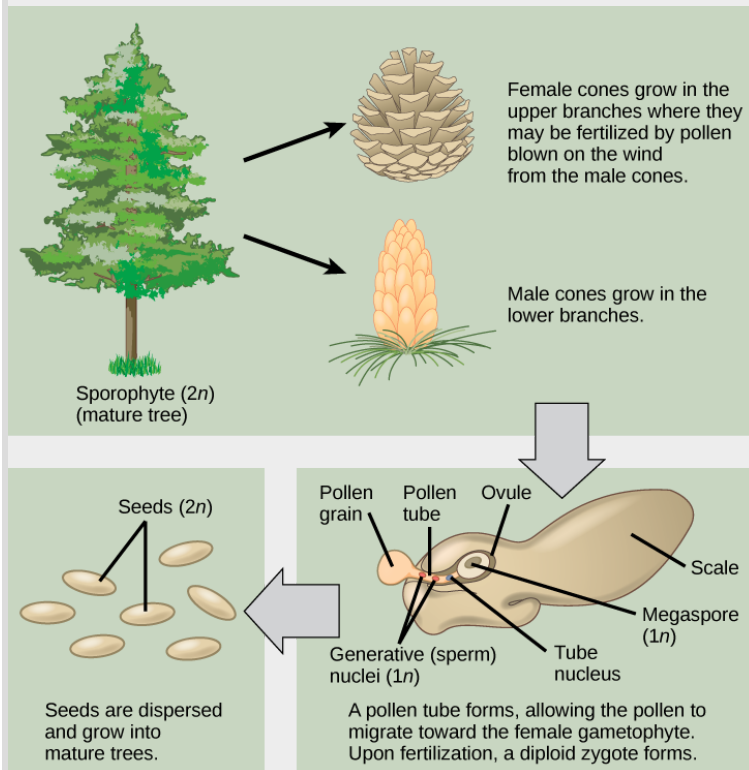
This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones.

At what stage does the diploid zygote form?

    a. when the female cone begins to bud from the tree
    b. at fertilization
    c. when the seeds drop from the tree

Diversity of Gymnosperms

Modern gymnosperms are classified into four phyla. Coniferophyta, Cycadophyta, and Ginkgophyta are similar in their production of secondary cambium (cells that generate the vascular system of the trunk or stem and are partially specialized for water transportation) and their pattern of seed development. However, the three phyla are not closely related phylogenetically to each other. Gnetophyta are considered the closest group to angiosperms because they produce true xylem tissue.

Conifers (Coniferophyta)

Conifers are the dominant phylum of gymnosperms, with the most variety of species ([link]). Most are typically tall trees that usually bear scale-like or needle-like leaves. Water evaporation from leaves is reduced by their thin shape and the thick cuticle. Snow slides easily off needle-shaped leaves, keeping the load light and decreasing breaking of branches. Adaptations to

cold and dry weather explain the predominance of conifers at high altitudes and in cold climates. Conifers include familiar evergreen trees such as pines, spruces, firs, cedars, sequoias, and yews. A few species are deciduous and lose their leaves in fall. The European larch and the tamarack are examples of deciduous conifers ([link]**c**). Many coniferous trees are harvested for paper pulp and timber. The wood of conifers is more primitive than the wood of angiosperms; it contains tracheids, but no vessel elements, and is therefore referred to as "soft wood."

Conifers are the dominant form of vegetation in cold or arid environments and at high altitudes. Shown here are the (a) evergreen spruce *Picea* sp., (b) juniper *Juniperus* sp., (c) sequoia *Sequoia Semervirens*, which is a deciduous gymnosperm, and (d) the tamarack *Larix larcinia*. Notice the yellow leaves of the tamarack. (credit a: modification of work by

Rosendahl; credit b: modification of work by
Alan Levine; credit c: modification of work by
Wendy McCormic; credit d: modification of
work by Micky Zlimen)

Cycads

Cycads thrive in mild climates, and are often mistaken for palms because of
the shape of their large, compound leaves. Cycads bear large cones ([link]),
and may be pollinated by beetles rather than wind: unusual for a
gymnosperm. They dominated the landscape during the age of dinosaurs in
the Mesozoic, but only a hundred or so species persisted to modern times.
They face possible extinction, and several species are protected through
international conventions. Because of their attractive shape, they are often
used as ornamental plants in gardens in the tropics and subtropics.

This *Encephalartos ferox* cycad
has large cones and broad, fern-
like leaves. (credit: Wendy Cutler)

Gingkophytes

The single surviving species of the **gingkophytes** group is the *Gingko biloba* ([link]). Its fan-shaped leaves—unique among seed plants because they feature a dichotomous venation pattern—turn yellow in autumn and fall from the tree. For centuries, *G. biloba* was cultivated by Chinese Buddhist monks in monasteries, which ensured its preservation. It is planted in public spaces because it is unusually resistant to pollution. Male and female organs are produced on separate plants. Typically, gardeners plant only male trees because the seeds produced by the female plant have an off-putting smell of rancid butter.

This plate from the 1870 book *Flora Japonica, Sectio Prima (Tafelband)* depicts the

leaves and fruit of *Gingko biloba*, as drawn by Philipp Franz von Siebold and Joseph Gerhard Zuccarini.

Gnetophytes

Gnetophytes are the closest relative to modern angiosperms, and include three dissimilar genera of plants: *Ephedra*, *Gnetum*, and *Welwitschia* ([link]). Like angiosperms, they have broad leaves. In tropical and subtropical zones, gnetophytes are vines or small shrubs. *Ephedra* occurs in dry areas of the West Coast of the United States and Mexico. *Ephedra*'s small, scale-like leaves are the source of the compound ephedrine, which is used in medicine as a potent decongestant. Because ephedrine is similar to amphetamines, both in chemical structure and neurological effects, its use is restricted to prescription drugs. Like angiosperms, but unlike other gymnosperms, all gnetophytes possess vessel elements in their xylem.

(a) *Ephedra*   (b) *Gnetum*   (c) *Welwitschia*

(a) *Ephedra viridis*, known by the common name *Mormon tea*, grows on the West Coast of the United States and Mexico. (b) *Gnetum gnemon* grows in Malaysia. (c) The large *Welwitschia mirabilis* can be found in the Namibian desert. (credit a: modification of work by USDA; credit b: modification of work

by Malcolm Manners; credit c: modification of work by Derek
Keats)

Section Summary

Gymnosperms are heterosporous seed plants that produce naked seeds.
They appeared in the Paleozoic period and were the dominant plant life
during the Mesozoic. Modern-day gymnosperms belong to four phyla. The
largest phylum, Coniferophyta, is represented by conifers, the predominant
plants at high altitude and latitude. Cycads (phylum Cycadophyta) resemble
palm trees and grow in tropical climates. *Gingko biloba* is the only
representative of the phylum Gingkophyta. The last phylum, Gnetophyta, is
a diverse group of shrubs that produce vessel elements in their wood.

Art Connections

Exercise:

Problem:[link] At what stage does the diploid zygote form?

a. When the female cone begins to bud from the tree
b. At fertilization
c. When the seeds drop from the tree
d. When the pollen tube begins to grow

Solution:

[link] B. The diploid zygote forms after the pollen tube has finished forming, so that the male generative nuclei can fuse with the female gametophyte.

Review Questions

Exercise:

Problem: Which of the following traits characterizes gymnosperms?

a. The plants carry exposed seeds on modified leaves.
b. Reproductive structures are located in a flower.
c. After fertilization, the ovary thickens and forms a fruit.
d. The gametophyte is longest phase of the life cycle.

Solution:

A

Exercise:

Problem:

Megasporocytes will eventually produce which of the following?

a. pollen grain
b. sporophytes
c. male gametophytes
d. female gametophytes

Solution:

D

Exercise:

Problem:

What is the ploidy of the following structures: gametophyte, seed, spore, sporophyte?

a. 1*n*, 1*n*, 2*n*, 2*n*
b. 1*n*, 2*n*, 1*n*, 2*n*
c. 2*n*, 1*n*, 2*n*, 1*n*
d. 2*n*, 2*n*, 1*n*, 1*n*

Solution:

B

Exercise:

Problem: In the northern forests of Siberia, a tall tree is most likely a:

a. conifer
b. cycad
c. *Gingko biloba*
d. gnetophyte

Solution:

A

Free Response

Exercise:

Problem:

The Mediterranean landscape along the sea shore is dotted with pines and cypresses. The weather is not cold, and the trees grow at sea level. What evolutionary adaptation of conifers makes them suitable to the Mediterranean climate?

Solution:

The trees are adapted to arid weather, and do not lose as much water due to transpiration as non-conifers.

Exercise:

Problem: What are the four modern-day phyla of gymnosperms?

Solution:

The four modern-day phyla of gymnosperms are Coniferophyta, Cycadophyta, Gingkophyta, and Gnetophyta.

Glossary

conifer
    dominant phylum of gymnosperms with the most variety of trees

cycad
    gymnosperm that grows in tropical climates and resembles a palm tree; member of the phylum Cycadophyta

dioecious
    describes a species in which the male and female reproductive organs are carried on separate specimens

gingkophyte

gymnosperm with one extant species, the *Gingko biloba*: a tree with fan-shaped leaves

gnetophyte

    gymnosperm shrub with varied morphological features that produces vessel elements in its woody tissues; the phylum includes the genera *Ephedra, Gnetum* and *Welwitschia*

gymnosperm

    seed plant with naked seeds (seeds exposed on modified leaves or in cones)

integument

    layer of sporophyte tissue that surrounds the megasporangium, and later, the embryo

megasporocyte

    megaspore mother cell; larger spore that germinates into a female gametophyte in a heterosporous plant

microsporocyte

    smaller spore that produces a male gametophyte in a heterosporous plant

monoecious

    describes a species in which the male and female reproductive organs are on the same plant

ovulate cone

    cone containing two ovules per scale

strobilus

    plant structure with a tight arrangement of sporophylls around a central stalk, as seen in cones or flowers; the male strobilus produces pollen, and the female strobilus produces eggs

Angiosperms

By the end of this section, you will be able to:

- Explain why angiosperms are the dominant form of plant life in most terrestrial ecosystems
- Describe the main parts of a flower and their purpose
- Detail the life cycle of an angiosperm
- Discuss the two main groups of flowering plants

From their humble and still obscure beginning during the early Jurassic period, the angiosperms—or flowering plants—have evolved to dominate most terrestrial ecosystems ([link]). With more than 250,000 species, the angiosperm phylum (Anthophyta) is second only to insects in terms of diversification.

These flowers grow in a botanical garden border in Bellevue, WA. Flowering plants dominate terrestrial landscapes. The vivid colors of flowers are an adaptation to pollination by animals such as insects and birds. (credit: Myriam Feldman)

The success of angiosperms is due to two novel reproductive structures: flowers and fruit. The function of the flower is to ensure pollination. Flowers also provide protection for the ovule and developing embryo inside a receptacle. The function of the fruit is seed dispersal. They also protect the developing seed. Different fruit structures or tissues on fruit—such as sweet flesh, wings, parachutes, or spines that grab—reflect the dispersal strategies that help spread seeds.

Flowers

Flowers are modified leaves, or sporophylls, organized around a central stalk. Although they vary greatly in appearance, all flowers contain the same structures: sepals, petals, carpels, and stamens. The peduncle attaches the flower to the plant. A whorl of **sepals** (collectively called the **calyx**) is located at the base of the peduncle and encloses the unopened floral bud. Sepals are usually photosynthetic organs, although there are some exceptions. For example, the corolla in lilies and tulips consists of three sepals and three petals that look virtually identical. **Petals**, collectively the **corolla**, are located inside the whorl of sepals and often display vivid colors to attract pollinators. Flowers pollinated by wind are usually small, feathery, and visually inconspicuous. Sepals and petals together form the **perianth**. The sexual organs (carpels and stamens) are located at the center of the flower.

As illustrated in [link], styles, stigmas, and ovules constitute the female organ: the **gynoecium** or **carpel**. Flower structure is very diverse, and carpels may be singular, multiple, or fused. Multiple fused carpels comprise a **pistil**. The megaspores and the female gametophytes are produced and protected by the thick tissues of the carpel. A long, thin structure called a **style** leads from the sticky **stigma**, where pollen is deposited, to the **ovary**, enclosed in the carpel. The ovary houses one or more ovules, each of which will develop into a seed upon fertilization. The male reproductive organs, the **stamens** (collectively called the androecium), surround the central carpel. Stamens are composed of a thin stalk called a **filament** and a sac-like structure called the anther. The filament supports the **anther**, where the microspores are produced by meiosis and develop into pollen grains.
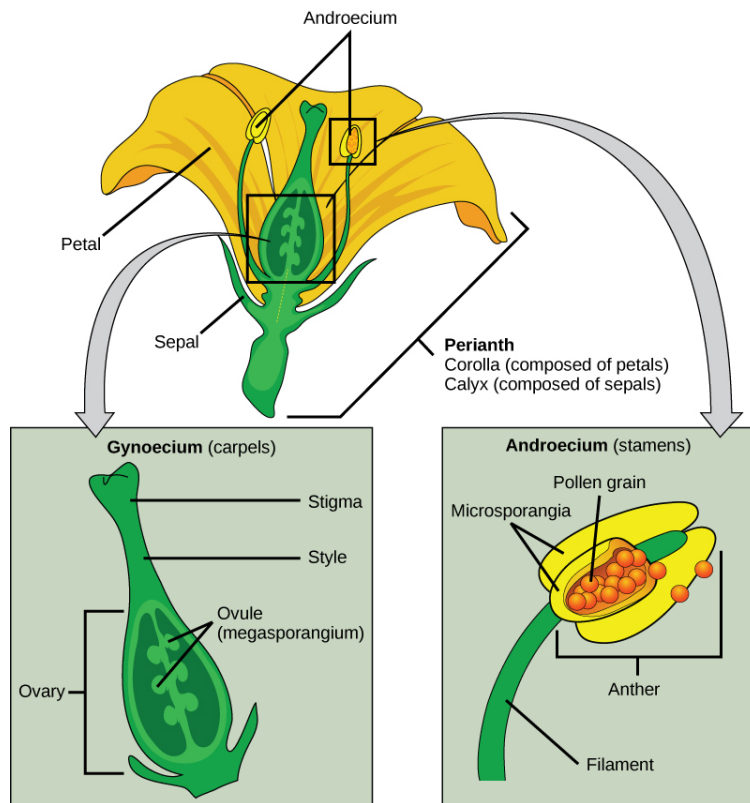
This image depicts the structure of a perfect flower. Perfect flowers produce both male and female floral organs. The flower shown has only one carpel, but some flowers have a cluster of carpels. Together, all the carpels make up the gynoecium. (credit: modification of work by Mariana Ruiz Villareal)

Fruit

As the seed develops, the walls of the ovary thicken and form the fruit. The seed forms in an ovary, which also enlarges as the seeds grow. In botany, a fertilized and fully grown, ripened ovary is a fruit. Many foods commonly called vegetables are actually fruit. Eggplants, zucchini, string beans, and bell peppers are all technically fruit because they contain seeds and are

derived from the thick ovary tissue. Acorns are nuts, and winged maple whirligigs (whose botanical name is samara) are also fruit. Botanists classify fruit into more than two dozen different categories, only a few of which are actually fleshy and sweet.

Mature fruit can be fleshy or dry. Fleshy fruit include the familiar berries, peaches, apples, grapes, and tomatoes. Rice, wheat, and nuts are examples of dry fruit. Another distinction is that not all fruits are derived from the ovary. For instance, strawberries are derived from the receptacle and apples from the pericarp, or hypanthium. Some fruits are derived from separate ovaries in a single flower, such as the raspberry. Other fruits, such as the pineapple, form from clusters of flowers. Additionally, some fruits, like watermelon and orange, have rinds. Regardless of how they are formed, fruits are an agent of seed dispersal. The variety of shapes and characteristics reflect the mode of dispersal. Wind carries the light dry fruit of trees and dandelions. Water transports floating coconuts. Some fruits attract herbivores with color or perfume, or as food. Once eaten, tough, undigested seeds are dispersed through the herbivore's feces. Other fruits have burs and hooks to cling to fur and hitch rides on animals.

The Life Cycle of an Angiosperm

The adult, or sporophyte, phase is the main phase of an angiosperm's life cycle ([link]). Like gymnosperms, angiosperms are heterosporous. Therefore, they generate microspores, which will generate pollen grains as the male gametophytes, and megaspores, which will form an ovule that contains female gametophytes. Inside the anthers' microsporangia, male gametophytes divide by meiosis to generate haploid microspores, which, in turn, undergo mitosis and give rise to pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm and a second cell that will become the pollen tube cell.

Note:
Art Connection
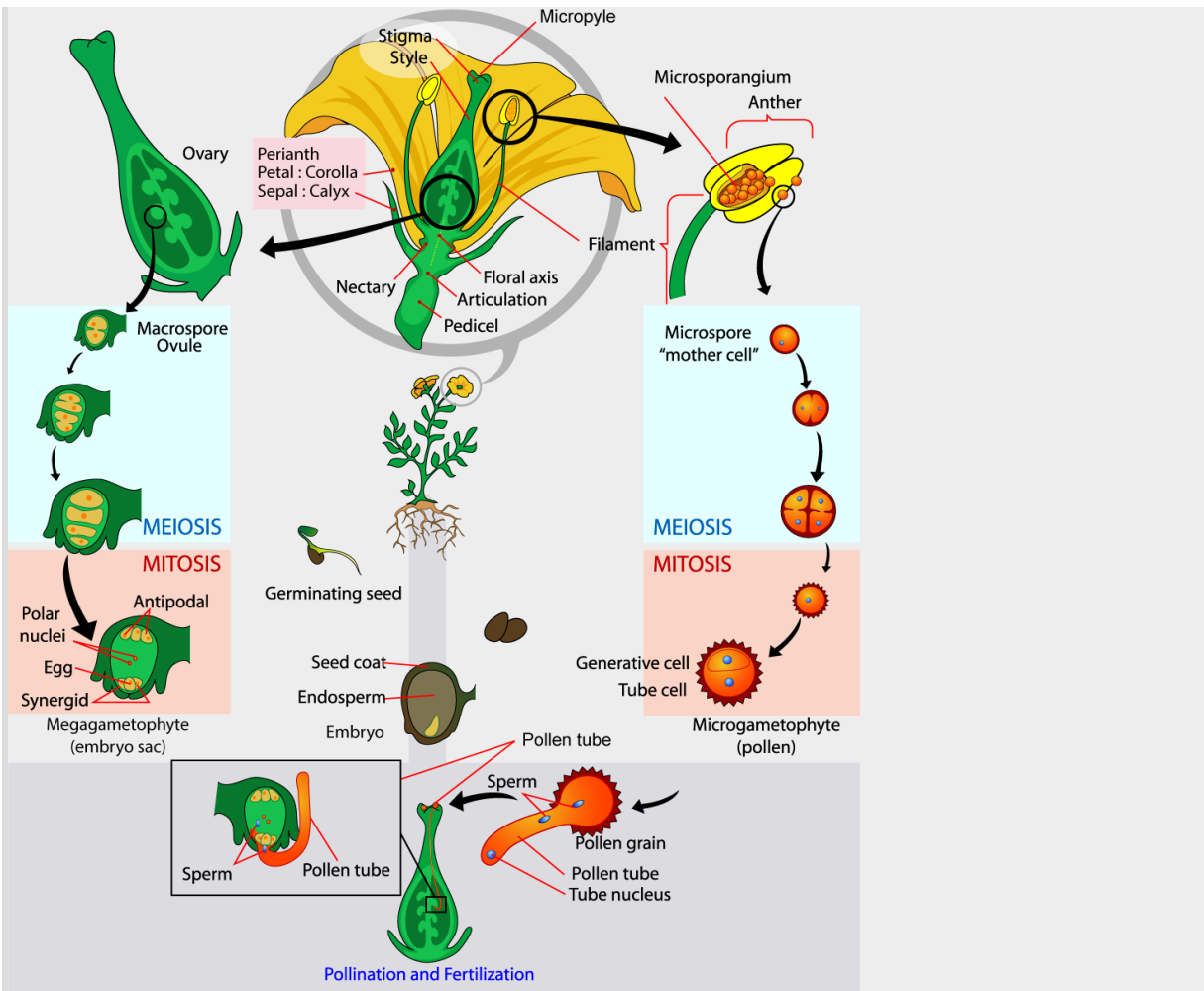
The life cycle of an angiosperm is shown. Anthers and carpels are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms. (credit: modification of work by Mariana Ruiz Villareal)

If a flower lacked a megasporangium, what type of gamete would not form? If the flower lacked a microsporangium, what type of gamete would not form?

The ovule, sheltered within the ovary of the carpel, contains the megasporangium protected by two layers of integuments and the ovary wall. Within each megasporangium, a megasporocyte undergoes meiosis, generating four megaspores—three small and one large. Only the large megaspore survives; it produces the female gametophyte, referred to as the embryo sac. The megaspore divides three times to form an eight-cell stage. Four of these cells migrate to each pole of the embryo sac; two come to the equator, and will eventually fuse to form a $2n$ polar nucleus; the three cells away from the egg form antipodals, and the two cells closest to the egg become the synergids.

The mature embryo sac contains one egg cell, two synergids or "helper" cells, three antipodal cells, and two polar nuclei in a central cell. When a pollen grain reaches the stigma, a pollen tube extends from the grain, grows down the style, and enters through the micropyle: an opening in the integuments of the ovule. The two sperm cells are deposited in the embryo sac.

A double fertilization event then occurs. One sperm and the egg combine, forming a diploid zygote—the future embryo. The other sperm fuses with the $2n$ polar nuclei, forming a triploid cell that will develop into the endosperm, which is tissue that serves as a food reserve. The zygote develops into an embryo with a radicle, or small root, and one (monocot) or two (dicot) leaf-like organs called **cotyledons**. This difference in the number of embryonic leaves is the basis for the two major groups of angiosperms: the monocots and the eudicots. Seed food reserves are stored outside the embryo, in the form of complex carbohydrates, lipids or proteins. The cotyledons serve as conduits to transmit the broken-down food reserves from their storage site inside the seed to the developing embryo. The seed consists of a toughened layer of integuments forming the coat, the endosperm with food reserves, and at the center, the well-protected embryo.

Most flowers are monoecious or bisexual, which means that they carry both stamens and carpels; only a few species self-pollinate. Monoecious flowers are also known as "perfect" flowers because they contain both types of sex organs ([link]). Both anatomical and environmental barriers promote cross-

pollination mediated by a physical agent (wind or water), or an animal, such as an insect or bird. Cross-pollination increases genetic diversity in a species.

Diversity of Angiosperms

Angiosperms are classified in a single phylum: the **Anthophyta**. Modern angiosperms appear to be a monophyletic group, which means that they originate from a single ancestor. Flowering plants are divided into two major groups, according to the structure of the cotyledons, pollen grains, and other structures. **Monocots** include grasses and lilies, and eudicots or **dicots** form a polyphyletic group. **Basal angiosperms** are a group of plants that are believed to have branched off before the separation into monocots and eudicots because they exhibit traits from both groups. They are categorized separately in many classification schemes. The *Magnoliidae* (magnolia trees, laurels, and water lilies) and the *Piperaceae* (peppers) belong to the basal angiosperm group.

Basal Angiosperms

The Magnoliidae are represented by the magnolias: tall trees bearing large, fragrant flowers that have many parts and are considered archaic ([link]**d**). Laurel trees produce fragrant leaves and small, inconspicuous flowers. The *Laurales* grow mostly in warmer climates and are small trees and shrubs. Familiar plants in this group include the bay laurel, cinnamon, spice bush ([link]**a**), and avocado tree. The *Nymphaeales* are comprised of the water lilies, lotus ([link]**c**), and similar plants; all species thrive in freshwater biomes, and have leaves that float on the water surface or grow underwater. Water lilies are particularly prized by gardeners, and have graced ponds and pools for thousands of years. The *Piperales* are a group of herbs, shrubs, and small trees that grow in the tropical climates. They have small flowers without petals that are tightly arranged in long spikes. Many species are the source of prized fragrance or spices, for example the berries of *Piper nigrum* ([link]**b**) are the familiar black peppercorns that are used to flavor many dishes.

The (a) common spicebush belongs to the *Laurales*, the same family as cinnamon and bay laurel. The fruit of (b) the *Piper nigrum* plant is black pepper, the main product that was traded along spice routes. Notice the small, unobtrusive, clustered flowers. (c) Lotus flowers, *Nelumbo nucifera*, have been cultivated since ancient times for their ornamental value; the root of the lotus flower is eaten as a vegetable. The red seeds of (d) a magnolia tree, characteristic of the final stage, are just starting to appear. (credit a: modification of work by Cory Zanker; credit b: modification of work by Franz Eugen Köhler; credit c: modification of work by "berduchwal"/Flickr; credit d:

modification of work by "Coastside2"/Wikimedia Commons).

Monocots

Plants in the monocot group are primarily identified as such by the presence of a single cotyledon in the seedling. Other anatomical features shared by monocots include veins that run parallel to the length of the leaves, and flower parts that are arranged in a three- or six-fold symmetry. True woody tissue is rarely found in monocots. In palm trees, vascular and parenchyma tissues produced by the primary and secondary thickening meristems form the trunk. The pollen from the first angiosperms was monosulcate, containing a single furrow or pore through the outer layer. This feature is still seen in the modern monocots. Vascular tissue of the stem is not arranged in any particular pattern. The root system is mostly adventitious and unusually positioned, with no major tap root. The monocots include familiar plants such as the true lilies (which are at the origin of their alternate name of Liliopsida), orchids, grasses, and palms. Many important crops are monocots, such as rice and other cereals, corn, sugar cane, and tropical fruits like bananas and pineapples ([link]).

The world's major crops are flowering plants. (a) Rice, (b) wheat, and (c) bananas are monocots, while (d) cabbage, (e) beans, and (f) peaches are dicots. (credit a: modification of work by David Nance, USDA ARS; credit b, c: modification of work by Rosendahl; credit d: modification of work by Bill Tarpenning, USDA; credit e: modification of work by Scott Bauer, USDA ARS; credit f: modification of work by Keith Weller, USDA)

Eudicots

Eudicots, or true dicots, are characterized by the presence of two cotyledons in the developing shoot. Veins form a network in leaves, and flower parts come in four, five, or many whorls. Vascular tissue forms a ring in the stem; in monocots, vascular tissue is scattered in the stem. Eudicots can be **herbaceous** (like grasses), or produce woody tissues. Most eudicots produce pollen that is trisulcate or triporate, with three furrows or pores.

The root system is usually anchored by one main root developed from the embryonic radicle. Eudicots comprise two-thirds of all flowering plants. The major differences between monocots and eudicots are summarized in [link]. Many species exhibit characteristics that belong to either group; as such, the classification of a plant as a monocot or a eudicot is not always clearly evident.

Comparison of Structural Characteristics of Monocots and Eudicots		
Characteristic	**Monocot**	**Eudicot**
Cotyledon	One	Two
Veins in Leaves	Parallel	Network (branched)
Stem Vascular Tissue	Scattered	Arranged in ring pattern
Roots	Network of adventitious roots	Tap root with many lateral roots
Pollen	Monosulcate	Trisulcate
Flower Parts	Three or multiple of three	Four, five, multiple of four or five and whorls

Section Summary

Angiosperms are the dominant form of plant life in most terrestrial ecosystems, comprising about 90 percent of all plant species. Most crops and ornamental plants are angiosperms. Their success comes from two innovative structures that protect reproduction from variability in the environment: the flower and the fruit. Flowers were derived from modified leaves. The main parts of a flower are the sepals and petals, which protect the reproductive parts: the stamens and the carpels. The stamens produce the male gametes in pollen grains. The carpels contain the female gametes (the eggs inside the ovules), which are within the ovary of a carpel. The walls of the ovary thicken after fertilization, ripening into fruit that ensures dispersal by wind, water, or animals.

The angiosperm life cycle is dominated by the sporophyte stage. Double fertilization is an event unique to angiosperms. One sperm in the pollen fertilizes the egg, forming a diploid zygote, while the other combines with the two polar nuclei, forming a triploid cell that develops into a food storage tissue called the endosperm. Flowering plants are divided into two main groups, the monocots and eudicots, according to the number of cotyledons in the seedlings. Basal angiosperms belong to an older lineage than monocots and eudicots.

Art Connections

Exercise:

Problem:

[link] If a flower lacked a megasporangium, what type of gamete would not form? If the flower lacked a microsporangium, what type of gamete would not form?

Solution:

[link] Without a megasporangium, an egg would not form; without a microsporangium, pollen would not form.

Review Questions

Exercise:

Problem:

Which of the following structures in a flower is not directly involved in reproduction?

    a. the style
    b. the stamen
    c. the sepal
    d. the anther

Solution:

C

Exercise:

Problem: Pollen grains develop in which structure?

    a. the anther
    b. the stigma
    c. the filament
    d. the carpel

Solution:

A

Exercise:

Problem:

In the course of double fertilization, one sperm cell fuses with the egg and the second one fuses with _____.

    a. the synergids
    b. the polar nuclei of the center cell

c. the egg as well
d. the antipodal cells

Solution:

B

Exercise:

Problem:

Corn develops from a seedling with a single cotyledon, displays parallel veins on its leaves, and produces monosulcate pollen. It is most likely:

a. a gymnosperm
b. a monocot
c. a eudicot
d. a basal angiosperm

Solution:

B

Free Response

Exercise:

Problem:

Some cycads are considered endangered species and their trade is severely restricted. Customs officials stop suspected smugglers who claim that the plants in their possession are palm trees, not cycads. How would a botanist distinguish between the two types of plants?

Solution:

The resemblance between cycads and palm trees is only superficial. Cycads are gymnosperms and do not bear flowers or fruit. Cycads produce cones: large, female cones that produce naked seeds, and smaller male cones on separate plants. Palms do not.

Exercise:

Problem:

What are the two structures that allow angiosperms to be the dominant form of plant life in most terrestrial ecosystems?

Solution:

Angiosperms are successful because of flowers and fruit. These structures protect reproduction from variability in the environment.

Glossary

anther
> sac-like structure at the tip of the stamen in which pollen grains are produced

Anthophyta
> phylum to which angiosperms belong

basal angiosperms
> a group of plants that probably branched off before the separation of monocots and eudicots

calyx
> whorl of sepals

carpel
> single unit of the pistil

corolla
> collection of petals

cotyledon
    primitive leaf that develop in the zygote; monocots have one
    cotyledon, and dicots have two cotyledons

dicot
    (also, eudicot) related group of angiosperms whose embryos possess
    two cotyledons

filament
    thin stalk that links the anther to the base of the flower

gynoecium
    (also, carpel) structure that constitute the female reproductive organ

herbaceous
    grass-like plant noticeable by the absence of woody tissue

monocot
    related group of angiosperms that produce embryos with one cotyledon
    and pollen with a single ridge

ovary
    chamber that contains and protects the ovule or female
    megasporangium

perianth
    part of the plant consisting of the calyx (sepals) and corolla (petals)

petal
    modified leaf interior to the sepals; colorful petals attract animal
    pollinators

pistil
    fused group of carpels

sepal
    modified leaf that encloses the bud; outermost structure of a flower

stamen

structure that contains the male reproductive organs

stigma
uppermost structure of the carpel where pollen is deposited

style
long, thin structure that links the stigma to the ovary

The Role of Seed Plants
By the end of this section, you will be able to:

- Explain how angiosperm diversity is due, in part, to multiple interactions with animals
- Describe ways in which pollination occurs
- Discuss the roles that plants play in ecosystems and how deforestation threatens plant biodiversity

Without seed plants, life as we know it would not be possible. Plants play a key role in the maintenance of terrestrial ecosystems through stabilization of soils, cycling of carbon, and climate moderation. Large tropical forests release oxygen and act as carbon dioxide sinks. Seed plants provide shelter to many life forms, as well as food for herbivores, thereby indirectly feeding carnivores. Plant secondary metabolites are used for medicinal purposes and industrial production.

Animals and Plants: Herbivory

Coevolution of flowering plants and insects is a hypothesis that has received much attention and support, especially because both angiosperms and insects diversified at about the same time in the middle Mesozoic. Many authors have attributed the diversity of plants and insects to pollination and **herbivory**, or consumption of plants by insects and other animals. This is believed to have been as much a driving force as pollination. Coevolution of herbivores and plant defenses is observed in nature. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. A sort of arms race exists between plants and herbivores. To "combat" herbivores, some plant seeds—such as acorn and unripened persimmon—are high in alkaloids and therefore unsavory to some animals. Other plants are protected by bark, although some animals developed specialized mouth pieces to tear and chew vegetal material. Spines and thorns ([link]) deter most animals, except for mammals with thick fur, and some birds have specialized beaks to get past such defenses.

(a) Spines and (b) thorns are examples of plant defenses. (credit a: modification of work by Jon Sullivan; credit b: modification of work by I. Sáček, Sr.)

Herbivory has been used by seed plants for their own benefit in a display of mutualistic relationships. The dispersal of fruit by animals is the most striking example. The plant offers to the herbivore a nutritious source of food in return for spreading the plant's genetic material to a wider area.

An extreme example of collaboration between an animal and a plant is the case of acacia trees and ants. The trees support the insects with shelter and food. In return, ants discourage herbivores, both invertebrates and vertebrates, by stinging and attacking leaf-eating insects.

Animals and Plants: Pollination

Grasses are a successful group of flowering plants that are wind pollinated. They produce large amounts of powdery pollen carried over large distances by the wind. The flowers are small and wisp-like. Large trees such as oaks, maples, and birches are also wind pollinated.

Note:
Link to Learning

More than 80 percent of angiosperms depend on animals for **pollination**: the transfer of pollen from the anther to the stigma. Consequently, plants have developed many adaptations to attract pollinators. The specificity of specialized plant structures that target animals can be very surprising. It is possible, for example, to determine the type of pollinator favored by a plant just from the flower's characteristics. Many bird or insect-pollinated flowers secrete **nectar**, which is a sugary liquid. They also produce both fertile pollen, for reproduction, and sterile pollen rich in nutrients for birds and insects. Butterflies and bees can detect ultraviolet light. Flowers that attract these pollinators usually display a pattern of low ultraviolet reflectance that helps them quickly locate the flower's center and collect nectar while being dusted with pollen ([link]). Large, red flowers with little smell and a long funnel shape are preferred by hummingbirds, who have good color perception, a poor sense of smell, and need a strong perch. White flowers opened at night attract moths. Other animals—such as bats, lemurs, and lizards—can also act as pollinating agents. Any disruption to these interactions, such as the disappearance of bees as a consequence of colony collapse disorders, can lead to disaster for agricultural industries that depend heavily on pollinated crops.

As a bee collects nectar from a flower, it is dusted by pollen, which it then disperses to other flowers. (credit: John Severns)

Hypothesis: Because flies are drawn to other organisms based on smell and not sight, a flower that is normally attractive to bees because of its colors will attract flies if it is sprayed with polyamines similar to those generated by decaying flesh.

Test the hypothesis:

1. Select flowers usually pollinated by bees. White petunia may be good choice.
2. Divide the flowers into two groups, and while wearing eye protection and gloves, spray one group with a solution of either putrescine or cadaverine. (Putrescine dihydrochloride is typically available in 98 percent concentration; this can be diluted to approximately 50 percent for this experiment.)
3. Place the flowers in a location where flies are present, keeping the sprayed and unsprayed flowers separated.
4. Observe the movement of the flies for one hour. Record the number of visits to the flowers using a table similar to [link]. Given the rapid movement of flies, it may be beneficial to use a video camera to record the fly–flower interaction. Replay the video in slow motion to obtain an accurate record of the number of fly visits to the flowers.
5. Repeat the experiment four more times with the same species of flower, but using different specimens.
6. Repeat the entire experiment with a different type of flower that is normally pollinated by bees.

Results of Number of Visits by Flies to Sprayed and Control/Unsprayed Flowers

Trial #	Sprayed Flowers	Unsprayed Flowers
1		

Results of Number of Visits by Flies to Sprayed and Control/Unsprayed Flowers		
Trial #	Sprayed Flowers	Unsprayed Flowers
2		
3		
4		
5		

Analyze your data: Review the data you have recorded. Average the number of visits that flies made to sprayed flowers over the course of the five trials (on the first flower type) and compare and contrast them to the average number of visits that flies made to the unsprayed/control flowers. Can you draw any conclusions regarding the attraction of the flies to the sprayed flowers?

For the second flower type used, average the number of visits that flies made to sprayed flowers over the course of the five trials and compare and contrast them to the average number of visits that flies made to the unsprayed/control flowers. Can you draw any conclusions regarding the attraction of the flies to the sprayed flowers?

Compare and contrast the average number of visits that flies made to the two flower types. Can you draw any conclusions about whether the appearance of the flower had any impact on the attraction of flies? Did smell override any appearance differences, or were the flies attracted to one flower type more than another?

Form a conclusion: Do the results support the hypothesis? If not, how can this be explained?

The Importance of Seed Plants in Human Life

Seed plants are the foundation of human diets across the world ([link]). Many societies eat almost exclusively vegetarian fare and depend solely on seed plants for their nutritional needs. A few **crops** (rice, wheat, and potatoes) dominate the agricultural landscape. Many crops were developed during the agricultural revolution, when human societies made the transition from nomadic hunter–gatherers to horticulture and agriculture. Cereals, rich in carbohydrates, provide the staple of many human diets. Beans and nuts supply proteins. Fats are derived from crushed seeds, as is the case for peanut and rapeseed (canola) oils, or fruits such as olives. Animal husbandry also consumes large amounts of crops.

Staple crops are not the only food derived from seed plants. Fruits and vegetables provide nutrients, vitamins, and fiber. Sugar, to sweeten dishes, is produced from the monocot sugarcane and the eudicot sugar beet. Drinks are made from infusions of tea leaves, chamomile flowers, crushed coffee beans, or powdered cocoa beans. Spices come from many different plant parts: saffron and cloves are stamens and buds, black pepper and vanilla are seeds, the bark of a bush in the *Laurales* family supplies cinnamon, and the herbs that flavor many dishes come from dried leaves and fruit, such as the pungent red chili pepper. The volatile oils of flowers and bark provide the scent of perfumes. Additionally, no discussion of seed plant contribution to human diet would be complete without the mention of alcohol. Fermentation of plant-derived sugars and starches is used to produce alcoholic beverages in all societies. In some cases, the beverages are derived from the fermentation of sugars from fruit, as with wines and, in other cases, from the fermentation of carbohydrates derived from seeds, as with beers.

Seed plants have many other uses, including providing wood as a source of timber for construction, fuel, and material to build furniture. Most paper is derived from the pulp of coniferous trees. Fibers of seed plants such as cotton, flax, and hemp are woven into cloth. Textile dyes, such as indigo, were mostly of plant origin until the advent of synthetic chemical dyes.

Lastly, it is more difficult to quantify the benefits of ornamental seed plants. These grace private and public spaces, adding beauty and serenity to human lives and inspiring painters and poets alike.

(a)

(b)

(c)

(d)

Humans rely on plants for a variety of reasons. (a) Cacao beans were introduced in Europe from the New World, where they were used by Mesoamerican civilizations. Combined with sugar, another plant product, chocolate is a popular food. (b) Flowers like the tulip are cultivated for their beauty. (c) Quinine, extracted from cinchona trees, is used to treat malaria, to reduce fever, and to alleviate pain. (d) This violin is made of wood. (credit a: modification of work by "Everjean"/Flickr; credit b:

modification of work by Rosendahl; credit c: modification of work by Franz Eugen Köhler)

The medicinal properties of plants have been known to human societies since ancient times. There are references to the use of plants' curative properties in Egyptian, Babylonian, and Chinese writings from 5,000 years ago. Many modern synthetic therapeutic drugs are derived or synthesized de novo from plant secondary metabolites. It is important to note that the same plant extract can be a therapeutic remedy at low concentrations, become an addictive drug at higher doses, and can potentially kill at high concentrations. [link] presents a few drugs, their plants of origin, and their medicinal applications.

Plant Origin of Medicinal Compounds and Medical Applications		
Plant	**Compound**	**Application**
Deadly nightshade (*Atropa belladonna*)	Atropine	Dilate eye pupils for eye exams
Foxglove (*Digitalis purpurea*)	Digitalis	Heart disease, stimulates heart beat
Yam (*Dioscorea* spp.)	Steroids	Steroid hormones: contraceptive pill and cortisone

Plant Origin of Medicinal Compounds and Medical Applications

Plant	Compound	Application
Ephedra (*Ephedra* spp.)	Ephedrine	Decongestant and bronchiole dilator
Pacific yew (*Taxus brevifolia*)	Taxol	Cancer chemotherapy; inhibits mitosis
Opium poppy (*Papaver somniferum*)	Opioids	Analgesic (reduces pain without loss of consciousness) and narcotic (reduces pain with drowsiness and loss of consciousness) in higher doses
Quinine tree (*Cinchona* spp.)	Quinine	Antipyretic (lowers body temperature) and antimalarial
Willow (*Salix* spp.)	Salicylic acid (aspirin)	Analgesic and antipyretic

Note:
Career Connection
Ethnobotanist
The relatively new field of ethnobotany studies the interaction between a particular culture and the plants native to the region. Seed plants have a large influence on day-to-day human life. Not only are plants the major source of food and medicine, they also influence many other aspects of society, from clothing to industry. The medicinal properties of plants were

recognized early on in human cultures. From the mid-1900s, synthetic chemicals began to supplant plant-based remedies.

Pharmacognosy is the branch of pharmacology that focuses on medicines derived from natural sources. With massive globalization and industrialization, there is a concern that much human knowledge of plants and their medicinal purposes will disappear with the cultures that fostered them. This is where ethnobotanists come in. To learn about and understand the use of plants in a particular culture, an ethnobotanist must bring in knowledge of plant life and an understanding and appreciation of diverse cultures and traditions. The Amazon forest is home to an incredible diversity of vegetation and is considered an untapped resource of medicinal plants; yet, both the ecosystem and its indigenous cultures are threatened with extinction.

To become an ethnobotanist, a person must acquire a broad knowledge of plant biology, ecology and sociology. Not only are the plant specimens studied and collected, but also the stories, recipes, and traditions that are linked to them. For ethnobotanists, plants are not viewed solely as biological organisms to be studied in a laboratory, but as an integral part of human culture. The convergence of molecular biology, anthropology, and ecology make the field of ethnobotany a truly multidisciplinary science.

Biodiversity of Plants

Biodiversity ensures a resource for new food crops and medicines. Plant life balances ecosystems, protects watersheds, mitigates erosion, moderates climate and provides shelter for many animal species. Threats to plant diversity, however, come from many angles. The explosion of the human population, especially in tropical countries where birth rates are highest and economic development is in full swing, is leading to human encroachment into forested areas. To feed the larger population, humans need to obtain arable land, so there is massive clearing of trees. The need for more energy to power larger cities and economic growth therein leads to the construction of dams, the consequent flooding of ecosystems, and increased emissions of pollutants. Other threats to tropical forests come from poachers, who log trees for their precious wood. Ebony and Brazilian rosewood, both on the

endangered list, are examples of tree species driven almost to extinction by indiscriminate logging.

The number of plant species becoming extinct is increasing at an alarming rate. Because ecosystems are in a delicate balance, and seed plants maintain close symbiotic relationships with animals—whether predators or pollinators—the disappearance of a single plant can lead to the extinction of connected animal species. A real and pressing issue is that many plant species have not yet been catalogued, and so their place in the ecosystem is unknown. These unknown species are threatened by logging, habitat destruction, and loss of pollinators. They may become extinct before we have the chance to begin to understand the possible impacts from their disappearance. Efforts to preserve biodiversity take several lines of action, from preserving heirloom seeds to barcoding species. **Heirloom seeds** come from plants that were traditionally grown in human populations, as opposed to the seeds used for large-scale agricultural production. **Barcoding** is a technique in which one or more short gene sequences, taken from a well-characterized portion of the genome, are used to identify a species through DNA analysis.

Section Summary

Angiosperm diversity is due in part to multiple interactions with animals. Herbivory has favored the development of defense mechanisms in plants, and avoidance of those defense mechanism in animals. Pollination (the transfer of pollen to a carpel) is mainly carried out by wind and animals, and angiosperms have evolved numerous adaptations to capture the wind or attract specific classes of animals.

Plants play a key role in ecosystems. They are a source of food and medicinal compounds, and provide raw materials for many industries. Rapid deforestation and industrialization, however, threaten plant biodiversity. In turn, this threatens the ecosystem.

Review Questions

Exercise:

Problem:

Which of the following plant structures is not a defense against herbivory?

   a. thorns
   b. spines
   c. nectar
   d. alkaloids

Solution:

C

Exercise:

Problem:

White and sweet-smelling flowers with abundant nectar are probably pollinated by

   a. bees and butterflies
   b. flies
   c. birds
   d. wind

Solution:

A

Exercise:

Problem:

Abundant and powdery pollen produced by small, indistinct flowers is probably transported by:

   a. bees and butterflies

b. flies
c. birds
d. wind

Solution:

D

Exercise:

Problem: Plants are a source of _____.

a. food
b. fuel
c. medicine
d. all of the above

Solution:

D

Free Response

Exercise:

Problem:

Biosynthesis of nectar and nutrient-rich pollen is energetically very expensive for a plant. Yet, plants funnel large amounts of energy into animal pollination. What are the evolutionary advantages that offset the cost of attracting animal pollinators?

Solution:

Using animal pollinators promotes cross-pollination and increases genetic diversity. The odds that the pollen will reach another flower are

greatly increased compared with the randomness of wind pollination.

Exercise:

Problem:

What is biodiversity and why is it important to an ecosystem?

Solution:

Biodiversity is the variation in all forms of life. It can refer to variation within a species, within an ecosystem, or on an entire planet. It is important because it ensures a resource for new food crops and medicines. Plant life balances the ecosystems, protects watersheds, mitigates erosion, moderates climate, and provides shelter for many animal species.

Glossary

barcoding
    molecular biology technique in which one or more short gene sequences taken from a well-characterized portion of the genome is used to identify a species

crop
    cultivated plant

heirloom seed
    seed from a plant that was grown historically, but has not been used in modern agriculture on a large scale

herbivory
    consumption of plants by insects and other animals

nectar
    liquid rich in sugars produced by flowers to attract animal pollinators

pollination

transfer of pollen from the anther to the stigma

Introduction class="introduction"

A locust leaf consists of leaflets arrayed along a central midrib. Each leaflet is a complex photosynthetic machine, exquisitely adapted to capture sunlight and carbon dioxide. An intricate vascular system supplies the leaf with water and minerals, and exports the products of photosynthesis. (credit: modification of work by Todd Petit)

Plants are as essential to human existence as land, water, and air. Without plants, our day-to-day lives would be impossible because without oxygen from photosynthesis, aerobic life cannot be sustained. From providing food and shelter to serving as a source of medicines, oils, perfumes, and industrial products, plants provide humans with numerous valuable resources.

When you think of plants, most of the organisms that come to mind are vascular plants. These plants have tissues that conduct food and water, and they have seeds. Seed plants are divided into gymnosperms and angiosperms. Gymnosperms include the needle-leaved conifers—spruce, fir, and pine—as well as less familiar plants, such as ginkgos and cycads. Their seeds are not enclosed by a fleshy fruit. Angiosperms, also called flowering plants, constitute the majority of seed plants. They include broadleaved trees (such as maple, oak, and elm), vegetables (such as potatoes, lettuce, and carrots), grasses, and plants known for the beauty of their flowers (roses, irises, and daffodils, for example).

While individual plant species are unique, all share a common structure: a plant body consisting of stems, roots, and leaves. They all transport water, minerals, and sugars produced through photosynthesis through the plant body in a similar manner. All plant species also respond to environmental factors, such as light, gravity, competition, temperature, and predation.

The Plant Body
By the end of this section, you will be able to:

- Describe the shoot organ system and the root organ system
- Distinguish between meristematic tissue and permanent tissue
- Identify and describe the three regions where plant growth occurs
- Summarize the roles of dermal tissue, vascular tissue, and ground tissue
- Compare simple plant tissue with complex plant tissue

Like animals, plants contain cells with organelles in which specific metabolic activities take place. Unlike animals, however, plants use energy from sunlight to form sugars during photosynthesis. In addition, plant cells have cell walls, plastids, and a large central vacuole: structures that are not found in animal cells. Each of these cellular structures plays a specific role in plant structure and function.

> **Note:**
> Link to Learning
>
>
>
> Watch *Botany Without Borders*, a video produced by the Botanical Society of America about the importance of plants.

Plant Organ Systems

In plants, just as in animals, similar cells working together form a tissue. When different types of tissues work together to perform a unique function, they form an organ; organs working together form organ systems. Vascular

plants have two distinct organ systems: a shoot system, and a root system. The **shoot system** consists of two portions: the vegetative (non-reproductive) parts of the plant, such as the leaves and the stems, and the reproductive parts of the plant, which include flowers and fruits. The shoot system generally grows above ground, where it absorbs the light needed for photosynthesis. The **root system**, which supports the plants and absorbs water and minerals, is usually underground. [link] shows the organ systems of a typical plant.
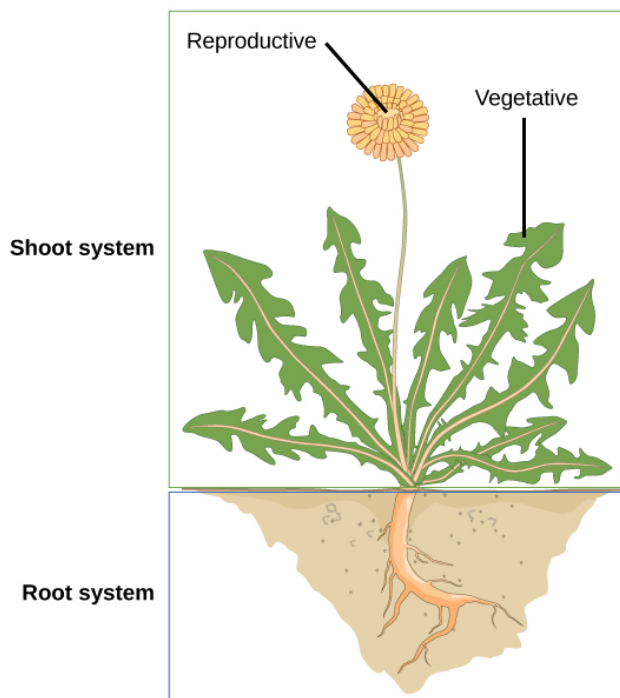
The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil.

Plant Tissues

Plants are multicellular eukaryotes with tissue systems made of various cell types that carry out specific functions. Plant tissue systems fall into one of two general types: meristematic tissue, and permanent (or non-meristematic) tissue. Cells of the meristematic tissue are found in **meristems**, which are plant regions of continuous cell division and growth. **Meristematic tissue** cells are either undifferentiated or incompletely differentiated, and they continue to divide and contribute to the growth of the plant. In contrast, **permanent tissue** consists of plant cells that are no longer actively dividing.

Meristematic tissues consist of three types, based on their location in the plant. **Apical meristems** contain meristematic tissue located at the tips of stems and roots, which enable a plant to extend in length. **Lateral meristems** facilitate growth in thickness or girth in a maturing plant. **Intercalary meristems** occur only in monocots, at the bases of leaf blades and at nodes (the areas where leaves attach to a stem). This tissue enables the monocot leaf blade to increase in length from the leaf base; for example, it allows lawn grass leaves to elongate even after repeated mowing.

Meristems produce cells that quickly differentiate, or specialize, and become permanent tissue. Such cells take on specific roles and lose their ability to divide further. They differentiate into three main types: dermal, vascular, and ground tissue. **Dermal tissue** covers and protects the plant, and **vascular tissue** transports water, minerals, and sugars to different parts of the plant. **Ground tissue** serves as a site for photosynthesis, provides a supporting matrix for the vascular tissue, and helps to store water and sugars.

Secondary tissues are either simple (composed of similar cell types) or complex (composed of different cell types). Dermal tissue, for example, is a simple tissue that covers the outer surface of the plant and controls gas exchange. Vascular tissue is an example of a complex tissue, and is made of two specialized conducting tissues: xylem and phloem. Xylem tissue transports water and nutrients from the roots to different parts of the plant, and includes three different cell types: vessel elements and tracheids (both of which conduct water), and xylem parenchyma. Phloem tissue, which transports organic compounds from the site of photosynthesis to other parts

of the plant, consists of four different cell types: sieve cells (which conduct photosynthates), companion cells, phloem parenchyma, and phloem fibers. Unlike xylem conducting cells, phloem conducting cells are alive at maturity. The xylem and phloem always lie adjacent to each other ([link]). In stems, the xylem and the phloem form a structure called a **vascular bundle**; in roots, this is termed the **vascular stele** or **vascular cylinder**.
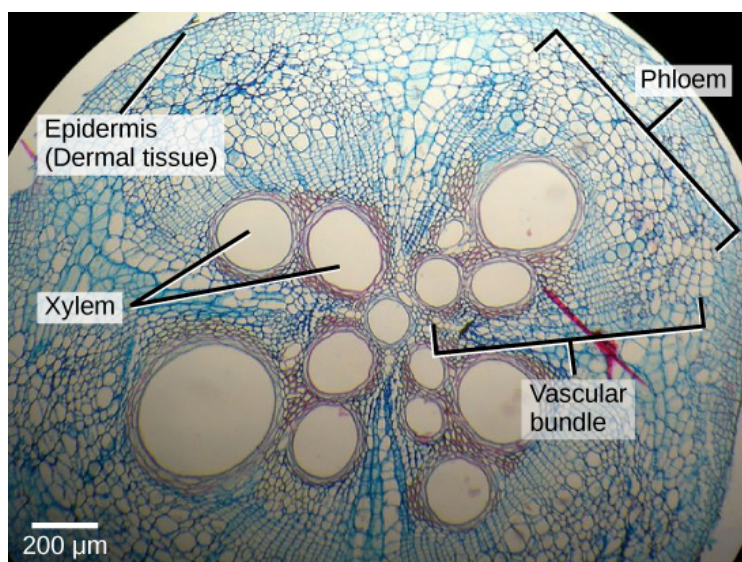
This light micrograph shows a cross section of a squash (*Cucurbita maxima*) stem. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest of the plant, are dead at functional maturity. Phloem cells, which transport sugars and other organic compounds from photosynthetic tissue to the rest of the plant, are living. The vascular bundles are encased in ground tissue and surrounded by dermal tissue. (credit: modification of work by "

Section Summary

A vascular plant consists of two organ systems: the shoot system and the root system. The shoot system includes the aboveground vegetative portions (stems and leaves) and reproductive parts (flowers and fruits). The root system supports the plant and is usually underground. A plant is composed of two main types of tissue: meristematic tissue and permanent tissue. Meristematic tissue consists of actively dividing cells found in root and shoot tips. As growth occurs, meristematic tissue differentiates into permanent tissue, which is categorized as either simple or complex. Simple tissues are made up of similar cell types; examples include dermal tissue and ground tissue. Dermal tissue provides the outer covering of the plant. Ground tissue is responsible for photosynthesis; it also supports vascular tissue and may store water and sugars. Complex tissues are made up of different cell types. Vascular tissue, for example, is made up of xylem and phloem cells.

Review Questions

Exercise:

Problem:

Plant regions of continuous growth are made up of _____.

    a. dermal tissue
    b. vascular tissue
    c. meristematic tissue
    d. permanent tissue

Solution:

C

Exercise:

Problem: Which of the following is the major site of photosynthesis?

a. apical meristem
b. ground tissue
c. xylem cells
d. phloem cells

Solution:

B

Free Response

Exercise:

Problem:

What type of meristem is found only in monocots, such as lawn grasses? Explain how this type of meristematic tissue is beneficial in lawn grasses that are mowed each week.

Solution:

Lawn grasses and other monocots have an intercalary meristem, which is a region of meristematic tissue at the base of the leaf blade. This is beneficial to the plant because it can continue to grow even when the tip of the plant is removed by grazing or mowing.

Exercise:

Problem:

Which plant part is responsible for transporting water, minerals, and sugars to different parts of the plant? Name the two types of tissue that make up this overall tissue, and explain the role of each.

Solution:

Vascular tissue transports water, minerals, and sugars throughout the plant. Vascular tissue is made up of xylem tissue and phloem tissue. Xylem tissue transports water and nutrients from the roots upward. Phloem tissue carries sugars from the sites of photosynthesis to the rest of the plant.

Glossary

apical meristem
  meristematic tissue located at the tips of stems and roots; enables a plant to extend in length

dermal tissue
  protective plant tissue covering the outermost part of the plant; controls gas exchange

ground tissue
  plant tissue involved in photosynthesis; provides support, and stores water and sugars

intercalary meristem
  meristematic tissue located at nodes and the bases of leaf blades; found only in monocots

lateral meristem
  meristematic tissue that enables a plant to increase in thickness or girth

meristematic tissue

tissue containing cells that constantly divide; contributes to plant growth

meristem
plant region of continuous growth

permanent tissue
plant tissue composed of cells that are no longer actively dividing

root system
belowground portion of the plant that supports the plant and absorbs water and minerals

shoot system
aboveground portion of the plant; consists of non-reproductive plant parts, such as leaves and stems, and reproductive parts, such as flowers and fruits

vascular bundle
strands of stem tissue made up of xylem and phloem

vascular stele
strands of root tissue made up of xylem and phloem

vascular tissue
tissue made up of xylem and phloem that transports food and water throughout the plant

Stems
By the end of this section, you will be able to:

- Describe the main function and basic structure of stems
- Compare and contrast the roles of dermal tissue, vascular tissue, and ground tissue
- Distinguish between primary growth and secondary growth in stems
- Summarize the origin of annual rings
- List and describe examples of modified stems

Stems are a part of the shoot system of a plant. They may range in length from a few millimeters to hundreds of meters, and also vary in diameter, depending on the plant type. Stems are usually above ground, although the stems of some plants, such as the potato, also grow underground. Stems may be herbaceous (soft) or woody in nature. Their main function is to provide support to the plant, holding leaves, flowers and buds; in some cases, stems also store food for the plant. A stem may be unbranched, like that of a palm tree, or it may be highly branched, like that of a magnolia tree. The stem of the plant connects the roots to the leaves, helping to transport absorbed water and minerals to different parts of the plant. It also helps to transport the products of photosynthesis, namely sugars, from the leaves to the rest of the plant.

Plant stems, whether above or below ground, are characterized by the presence of nodes and internodes ([link]). **Nodes** are points of attachment for leaves, aerial roots, and flowers. The stem region between two nodes is called an **internode**. The stalk that extends from the stem to the base of the leaf is the petiole. An **axillary bud** is usually found in the axil—the area between the base of a leaf and the stem—where it can give rise to a branch or a flower. The apex (tip) of the shoot contains the apical meristem within the **apical bud**.
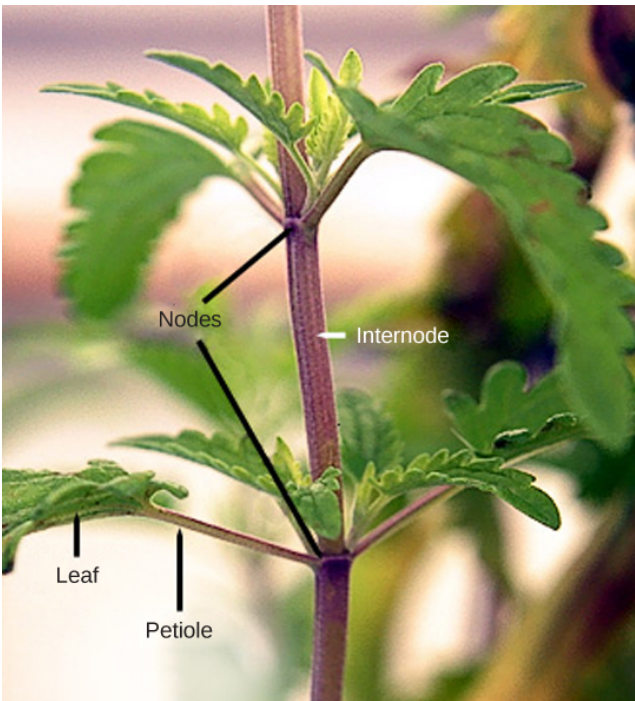
Leaves are attached to the plant stem at areas called nodes. An internode is the stem region between two nodes. The petiole is the stalk connecting the leaf to the stem. The leaves just above the nodes arose from axillary buds.

Stem Anatomy

The stem and other plant organs arise from the ground tissue, and are primarily made up of simple tissues formed from three types of cells: parenchyma, collenchyma, and sclerenchyma cells.

Parenchyma cells are the most common plant cells ([link]). They are found in the stem, the root, the inside of the leaf, and the pulp of the fruit. Parenchyma cells are responsible for metabolic functions, such as

photosynthesis, and they help repair and heal wounds. Some parenchyma cells also store starch.

The stem of common St John's Wort (*Hypericum perforatum*) is shown in cross section in this light micrograph. The central pith (greenish-blue, in the center) and peripheral cortex (narrow zone 3–5 cells thick just inside the epidermis) are composed of parenchyma cells. Vascular tissue composed of xylem (red) and phloem tissue (green, between the xylem and cortex) surrounds the pith. (credit: Rolf-Dieter Mueller)

Collenchyma cells are elongated cells with unevenly thickened walls ([link]). They provide structural support, mainly to the stem and leaves. These cells are alive at maturity and are usually found below the epidermis. The "strings" of a celery stalk are an example of collenchyma cells.
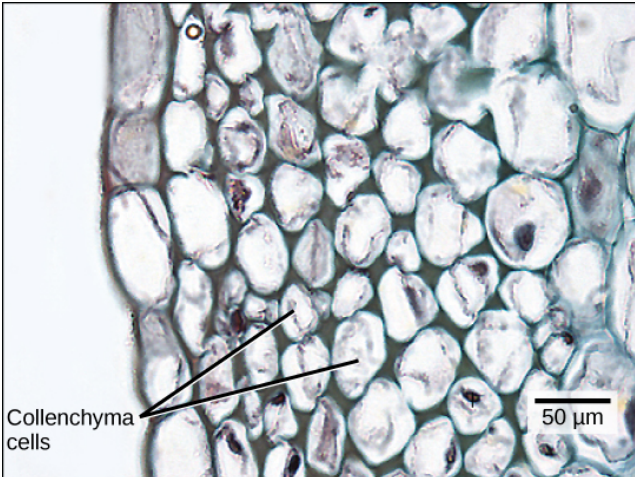
Collenchyma cell walls are uneven in thickness, as seen in this light micrograph. They provide support to plant structures. (credit: modification of work by Carl Szczerski; scale-bar data from Matt Russell)

Sclerenchyma cells also provide support to the plant, but unlike collenchyma cells, many of them are dead at maturity. There are two types of sclerenchyma cells: fibers and sclereids. Both types have secondary cell walls that are thickened with deposits of lignin, an organic compound that is a key component of wood. Fibers are long, slender cells; sclereids are smaller-sized. Sclereids give pears their gritty texture. Humans use sclerenchyma fibers to make linen and rope ([link]).

Note:
Art Connection
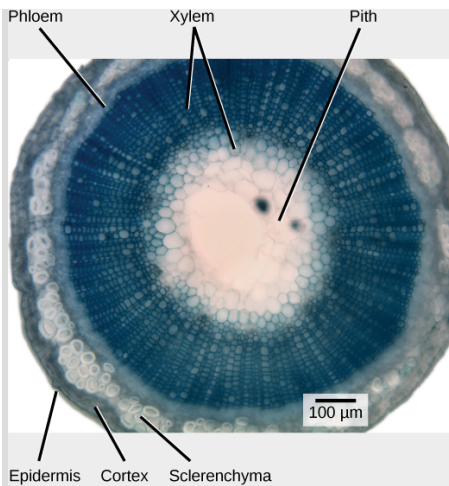
The central pith and outer cortex of the (a) flax stem are made up of parenchyma cells. Inside the cortex is a layer of sclerenchyma cells, which make up the fibers in flax rope and clothing. Humans have grown and harvested flax for thousands of years. In (b) this drawing, fourteenth-century women prepare linen. The (c) flax plant is grown and harvested for its fibers, which are used to weave linen, and for its seeds, which are the source of linseed oil. (credit a: modification of work by Emmanuel Boutet based on original work by Ryan R. MacKenzie; credit c: modification of work by Brian Dearth; scale-bar data from Matt Russell)

Which layers of the stem are made of parenchyma cells?

a. cortex and pith
b. phloem
c. sclerenchyma
d. xylem

Like the rest of the plant, the stem has three tissue systems: dermal, vascular, and ground tissue. Each is distinguished by characteristic cell types that perform specific tasks necessary for the plant's growth and survival.

Dermal Tissue

The dermal tissue of the stem consists primarily of **epidermis**, a single layer of cells covering and protecting the underlying tissue. Woody plants have a tough, waterproof outer layer of cork cells commonly known as **bark**, which further protects the plant from damage. Epidermal cells are the most numerous and least differentiated of the cells in the epidermis. The epidermis of a leaf also contains openings known as stomata, through which the exchange of gases takes place ([link]). Two cells, known as **guard cells**, surround each leaf stoma, controlling its opening and closing and thus regulating the uptake of carbon dioxide and the release of oxygen and water vapor. **Trichomes** are hair-like structures on the epidermal surface. They help to reduce **transpiration** (the loss of water by aboveground plant parts), increase solar reflectance, and store compounds that defend the leaves against predation by herbivores.
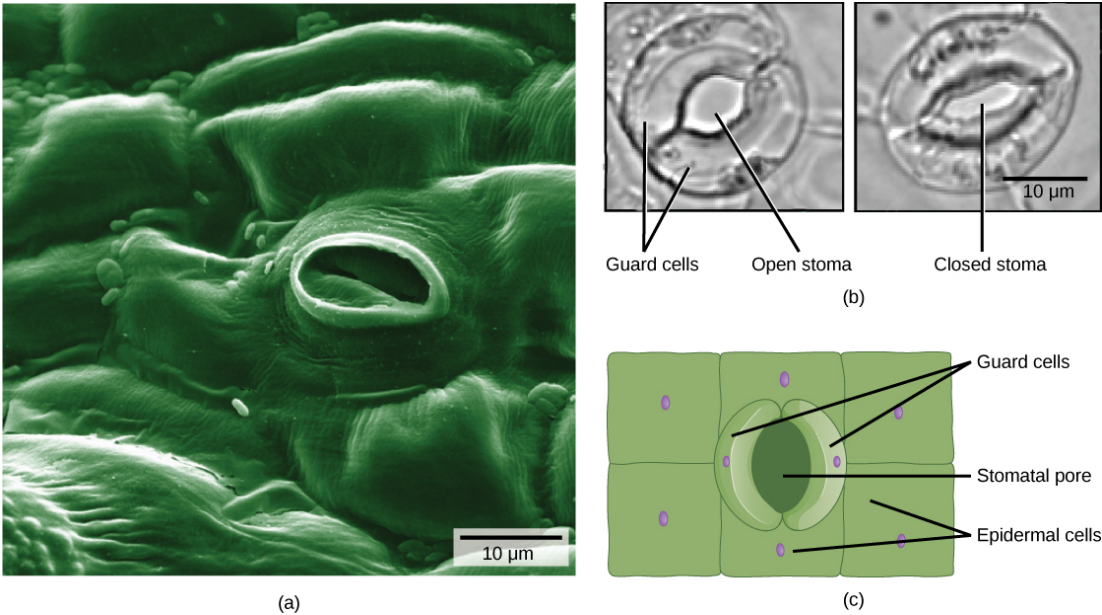
Openings called stomata (singular: stoma) allow a plant to take up carbon dioxide and release oxygen and water vapor. The (a) colorized scanning-electron micrograph shows a closed stoma of a dicot. Each stoma is flanked by two guard cells that regulate its (b) opening and closing. The (c) guard cells sit within the layer of epidermal cells (credit a: modification of work by Louisa Howard, Rippel Electron Microscope Facility, Dartmouth College; credit b: modification of work by June Kwak, University of Maryland; scale-bar data from Matt Russell)

Vascular Tissue

The xylem and phloem that make up the vascular tissue of the stem are arranged in distinct strands called vascular bundles, which run up and down the length of the stem. When the stem is viewed in cross section, the vascular bundles of dicot stems are arranged in a ring. In plants with stems that live for more than one year, the individual bundles grow together and

produce the characteristic growth rings. In monocot stems, the vascular bundles are randomly scattered throughout the ground tissue ([link]).

Dicot stem   **Monocot stem**

Sclerenchyma

Vascular bundle

Ground tissue
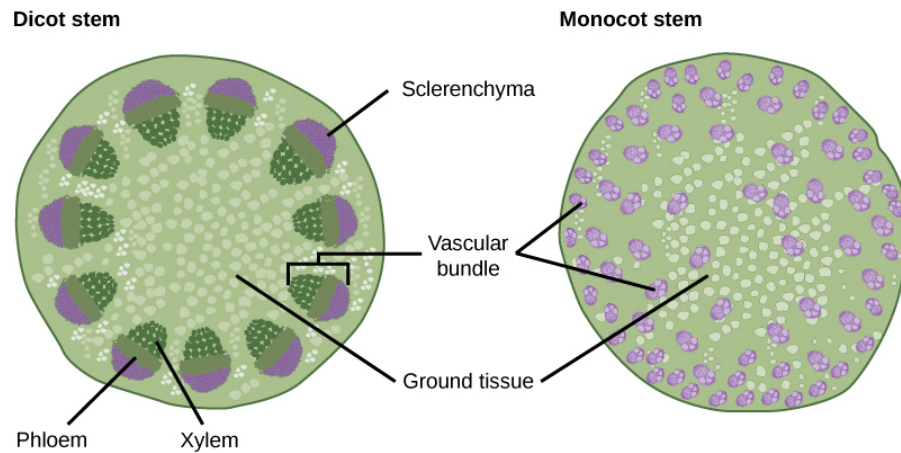
Phloem   Xylem

In (a) dicot stems, vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle, and phloem is located toward the exterior. Sclerenchyma fibers cap the vascular bundles. In (b) monocot stems, vascular bundles composed of xylem and phloem tissues are scattered throughout the ground tissue.

Xylem tissue has three types of cells: xylem parenchyma, tracheids, and vessel elements. The latter two types conduct water and are dead at maturity. **Tracheids** are xylem cells with thick secondary cell walls that are lignified. Water moves from one tracheid to another through regions on the side walls known as pits, where secondary walls are absent. **Vessel elements** are xylem cells with thinner walls; they are shorter than tracheids. Each vessel element is connected to the next by means of a perforation plate at the end walls of the element. Water moves through the perforation plates to travel up the plant.

Phloem tissue is composed of sieve-tube cells, companion cells, phloem parenchyma, and phloem fibers. A series of **sieve-tube cells** (also called sieve-tube elements) are arranged end to end to make up a long sieve tube, which transports organic substances such as sugars and amino acids. The sugars flow from one sieve-tube cell to the next through perforated sieve plates, which are found at the end junctions between two cells. Although still alive at maturity, the nucleus and other cell components of the sieve-tube cells have disintegrated. **Companion cells** are found alongside the sieve-tube cells, providing them with metabolic support. The companion cells contain more ribosomes and mitochondria than the sieve-tube cells, which lack some cellular organelles.

Ground Tissue

Ground tissue is mostly made up of parenchyma cells, but may also contain collenchyma and sclerenchyma cells that help support the stem. The ground tissue towards the interior of the vascular tissue in a stem or root is known as **pith**, while the layer of tissue between the vascular tissue and the epidermis is known as the **cortex**.

Growth in Stems

Growth in plants occurs as the stems and roots lengthen. Some plants, especially those that are woody, also increase in thickness during their life span. The increase in length of the shoot and the root is referred to as **primary growth**, and is the result of cell division in the shoot apical meristem. **Secondary growth** is characterized by an increase in thickness or girth of the plant, and is caused by cell division in the lateral meristem. [link] shows the areas of primary and secondary growth in a plant. Herbaceous plants mostly undergo primary growth, with hardly any secondary growth or increase in thickness. Secondary growth or "wood" is noticeable in woody plants; it occurs in some dicots, but occurs very rarely in monocots.
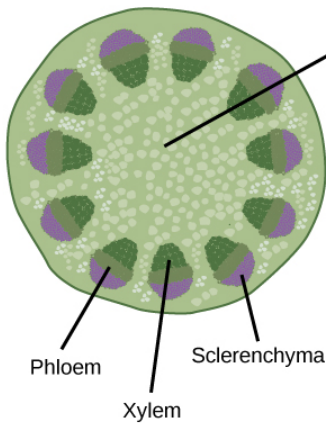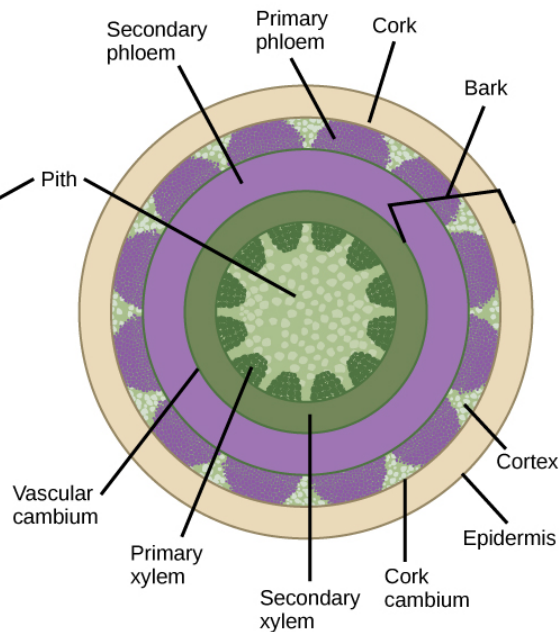
In woody plants, primary growth is followed by secondary growth, which allows the plant stem to increase in thickness or girth. Secondary vascular tissue is added as the plant grows, as well as a cork layer. The bark of a tree extends from the vascular cambium to the epidermis.

Some plant parts, such as stems and roots, continue to grow throughout a plant's life: a phenomenon called indeterminate growth. Other plant parts, such as leaves and flowers, exhibit determinate growth, which ceases when a plant part reaches a particular size.

Primary Growth

Most primary growth occurs at the apices, or tips, of stems and roots. Primary growth is a result of rapidly dividing cells in the apical meristems at the shoot tip and root tip. Subsequent cell elongation also contributes to

primary growth. The growth of shoots and roots during primary growth enables plants to continuously seek water (roots) or sunlight (shoots).

The influence of the apical bud on overall plant growth is known as apical dominance, which diminishes the growth of axillary buds that form along the sides of branches and stems. Most coniferous trees exhibit strong apical dominance, thus producing the typical conical Christmas tree shape. If the apical bud is removed, then the axillary buds will start forming lateral branches. Gardeners make use of this fact when they prune plants by cutting off the tops of branches, thus encouraging the axillary buds to grow out, giving the plant a bushy shape.

Note:
Link to Learning

Watch this [BBC Nature video](link) showing how time-lapse photography captures plant growth at high speed.

Secondary Growth

The increase in stem thickness that results from secondary growth is due to the activity of the lateral meristems, which are lacking in herbaceous plants. Lateral meristems include the vascular cambium and, in woody plants, the cork cambium (see [link]). The vascular cambium is located just outside the primary xylem and to the interior of the primary phloem. The cells of the vascular cambium divide and form secondary xylem (tracheids and vessel elements) to the inside, and secondary phloem (sieve elements and companion cells) to the outside. The thickening of the stem that occurs in

secondary growth is due to the formation of secondary phloem and secondary xylem by the vascular cambium, plus the action of cork cambium, which forms the tough outermost layer of the stem. The cells of the secondary xylem contain lignin, which provides hardiness and strength.

In woody plants, cork cambium is the outermost lateral meristem. It produces cork cells (bark) containing a waxy substance known as suberin that can repel water. The bark protects the plant against physical damage and helps reduce water loss. The cork cambium also produces a layer of cells known as phelloderm, which grows inward from the cambium. The cork cambium, cork cells, and phelloderm are collectively termed the **periderm**. The periderm substitutes for the epidermis in mature plants. In some plants, the periderm has many openings, known as **lenticels**, which allow the interior cells to exchange gases with the outside atmosphere ([link]). This supplies oxygen to the living and metabolically active cells of the cortex, xylem and phloem.

Lenticels on the bark of this cherry tree enable the woody stem to exchange gases with

the surrounding atmosphere.
(credit: Roger Griffith)

Annual Rings

The activity of the vascular cambium gives rise to annual growth rings. During the spring growing season, cells of the secondary xylem have a large internal diameter and their primary cell walls are not extensively thickened. This is known as early wood, or spring wood. During the fall season, the secondary xylem develops thickened cell walls, forming late wood, or autumn wood, which is denser than early wood. This alternation of early and late wood is due largely to a seasonal decrease in the number of vessel elements and a seasonal increase in the number of tracheids. It results in the formation of an annual ring, which can be seen as a circular ring in the cross section of the stem ([link]). An examination of the number of annual rings and their nature (such as their size and cell wall thickness) can reveal the age of the tree and the prevailing climatic conditions during each season.
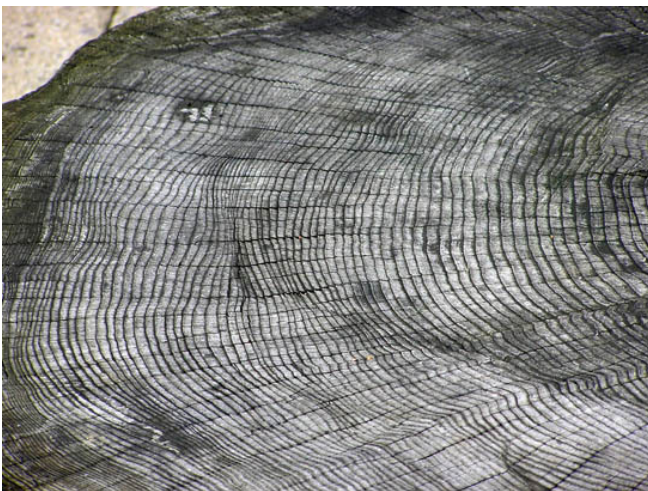
The rate of wood growth increases

in summer and decreases in winter,
producing a characteristic ring for
each year of growth. Seasonal
changes in weather patterns can
also affect the growth rate—note
how the rings vary in thickness.
(credit: Adrian Pingstone)

Stem Modifications

Some plant species have modified stems that are especially suited to a particular habitat and environment ([link]). A **rhizome** is a modified stem that grows horizontally underground and has nodes and internodes. Vertical shoots may arise from the buds on the rhizome of some plants, such as ginger and ferns. **Corms** are similar to rhizomes, except they are more rounded and fleshy (such as in gladiolus). Corms contain stored food that enables some plants to survive the winter. **Stolons** are stems that run almost parallel to the ground, or just below the surface, and can give rise to new plants at the nodes. **Runners** are a type of stolon that runs above the ground and produces new clone plants at nodes at varying intervals: strawberries are an example. **Tubers** are modified stems that may store starch, as seen in the potato (*Solanum* sp.). Tubers arise as swollen ends of stolons, and contain many adventitious or unusual buds (familiar to us as the "eyes" on potatoes). A **bulb**, which functions as an underground storage unit, is a modification of a stem that has the appearance of enlarged fleshy leaves emerging from the stem or surrounding the base of the stem, as seen in the iris.
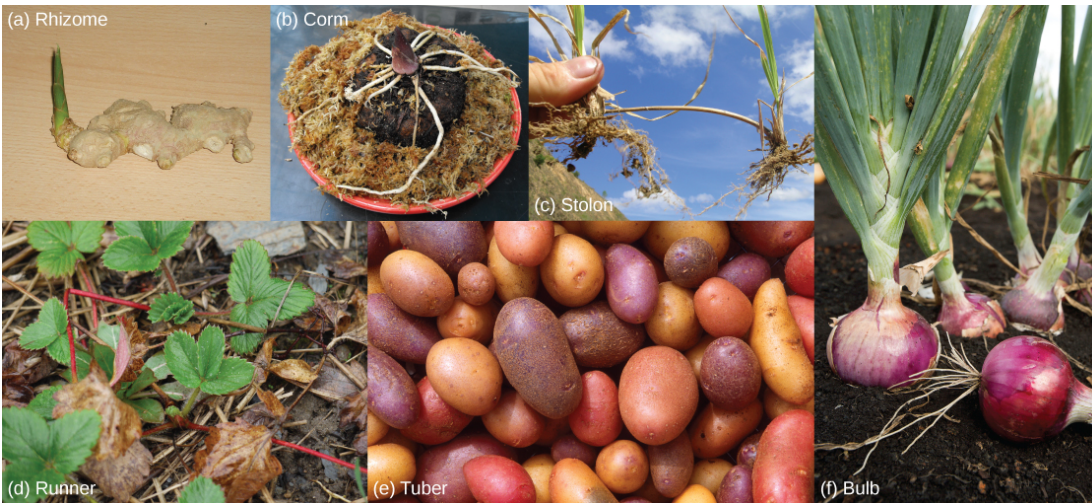
Stem modifications enable plants to thrive in a variety of environments. Shown are (a) ginger (*Zingiber officinale*) rhizomes, (b) a carrion flower (*Amorphophallus titanum*) corm (c) Rhodes grass (*Chloris gayana*) stolons, (d) strawberry (*Fragaria ananassa*) runners, (e) potato (*Solanum tuberosum*) tubers, and (f) red onion (*Allium*) bulbs. (credit a: modification of work by Maja Dumat; credit c: modification of work by Harry Rose; credit d: modification of work by Rebecca Siegel; credit e: modification of work by Scott Bauer, USDA ARS; credit f: modification of work by Stephen Ausmus, USDA ARS)

Watch botanist Wendy Hodgson, of Desert Botanical Garden in Phoenix, Arizona, explain how agave plants were cultivated for food hundreds of years ago in the Arizona desert in this [video:](#) *Finding the Roots of an Ancient Crop.*

Some aerial modifications of stems are tendrils and thorns ([[link]](#)). **Tendrils** are slender, twining strands that enable a plant (like a vine or pumpkin) to seek support by climbing on other surfaces. **Thorns** are modified branches appearing as sharp outgrowths that protect the plant; common examples include roses, Osage orange and devil's walking stick.

(a)   (b)

Found in southeastern United States, (a) buckwheat vine (*Brunnichia ovata*) is a weedy plant that climbs with the aid of tendrils. This one is shown climbing up a wooden stake. (b) Thorns are modified branches. (credit a: modification of work by Christopher Meloche, USDA ARS; credit b: modification of work by "macrophile"/Flickr)

Section Summary

The stem of a plant bears the leaves, flowers, and fruits. Stems are characterized by the presence of nodes (the points of attachment for leaves or branches) and internodes (regions between nodes).

Plant organs are made up of simple and complex tissues. The stem has three tissue systems: dermal, vascular, and ground tissue. Dermal tissue is the outer covering of the plant. It contains epidermal cells, stomata, guard cells, and trichomes. Vascular tissue is made up of xylem and phloem tissues and conducts water, minerals, and photosynthetic products. Ground tissue is responsible for photosynthesis and support and is composed of parenchyma, collenchyma, and sclerenchyma cells.

Primary growth occurs at the tips of roots and shoots, causing an increase in length. Woody plants may also exhibit secondary growth, or increase in thickness. In woody plants, especially trees, annual rings may form as growth slows at the end of each season. Some plant species have modified stems that help to store food, propagate new plants, or discourage predators. Rhizomes, corms, stolons, runners, tubers, bulbs, tendrils, and thorns are examples of modified stems.

Art Connections

Exercise:

Problem:

[link] Which layers of the stem are made of parenchyma cells?

    A. cortex and pith
    B. epidermis
    C. sclerenchyma
    D. epidermis and cortex.

Solution:

[link] A and B. The cortex, pith, and epidermis are made of parenchyma cells.

Review Questions

Exercise:

Problem:

Stem regions at which leaves are attached are called _____.

    a. trichomes
    b. lenticels
    c. nodes
    d. internodes

Solution:

C

Exercise:

Problem:

Which of the following cell types forms most of the inside of a plant?

    a. meristem cells
    b. collenchyma cells
    c. sclerenchyma cells
    d. parenchyma cells

Solution:

D

Exercise:

Problem:

Tracheids, vessel elements, sieve-tube cells, and companion cells are components of _____.

    a. vascular tissue
    b. meristematic tissue
    c. ground tissue
    d. dermal tissue

Solution:

A

Exercise:

Problem:

The primary growth of a plant is due to the action of the _____.

    a. lateral meristem
    b. vascular cambium
    c. apical meristem
    d. cork cambium

Solution:

C

Exercise:

Problem: Which of the following is an example of secondary growth?

    a. increase in length
    b. increase in thickness or girth
    c. increase in root hairs
    d. increase in leaf number

Solution:

B

Exercise:

Problem: Secondary growth in stems is usually seen in _____.

  a. monocots
  b. dicots
  c. both monocots and dicots
  d. neither monocots nor dicots

Solution:

B

Free Response

Exercise:

Problem:

Describe the roles played by stomata and guard cells. What would happen to a plant if these cells did not function correctly?

Solution:

Stomata allow gases to enter and exit the plant. Guard cells regulate the opening and closing of stomata. If these cells did not function correctly, a plant could not get the carbon dioxide needed for photosynthesis, nor could it release the oxygen produced by photosynthesis.

Exercise:

Problem:

Compare the structure and function of xylem to that of phloem.

Solution:

Xylem is made up tracheids and vessel elements, which are cells that transport water and dissolved minerals and that are dead at maturity. Phloem is made up of sieve-tube cells and companion cells, which transport carbohydrates and are alive at maturity.

Exercise:

Problem: Explain the role of the cork cambium in woody plants.

Solution:

In woody plants, the cork cambium is the outermost lateral meristem; it produces new cells towards the interior, which enables the plant to increase in girth. The cork cambium also produces cork cells towards the exterior, which protect the plant from physical damage while reducing water loss.

Exercise:

Problem: What is the function of lenticels?

Solution:

In woody stems, lenticels allow internal cells to exchange gases with the outside atmosphere.

Exercise:

Problem:

Besides the age of a tree, what additional information can annual rings reveal?

Solution:

Annual rings can also indicate the climate conditions that prevailed during each growing season.

Exercise:

Problem:

Give two examples of modified stems and explain how each example benefits the plant.

Solution:

Answers will vary. Rhizomes, stolons, and runners can give rise to new plants. Corms, tubers, and bulbs can also produce new plants and can store food. Tendrils help a plant to climb, while thorns discourage herbivores.

Glossary

apical bud
 bud formed at the tip of the shoot

axillary bud
 bud located in the axil: the stem area where the petiole connects to the stem

bark
 tough, waterproof, outer epidermal layer of cork cells

bulb
 modified underground stem that consists of a large bud surrounded by numerous leaf scales

collenchyma cell
 elongated plant cell with unevenly thickened walls; provides structural support to the stem and leaves

companion cell

> phloem cell that is connected to sieve-tube cells; has large amounts of ribosomes and mitochondrion

corm

> rounded, fleshy underground stem that contains stored food

cortex

> ground tissue found between the vascular tissue and the epidermis in a stem or root

epidermis

> single layer of cells found in plant dermal tissue; covers and protects underlying tissue

guard cells

> paired cells on either side of a stoma that control stomatal opening and thereby regulate the movement of gases and water vapor

internode

> region between nodes on the stem

lenticel

> opening on the surface of mature woody stems that facilitates gas exchange

node

> point along the stem at which leaves, flowers, or aerial roots originate

parenchyma cell

> most common type of plant cell; found in the stem, root, leaf, and in fruit pulp; site of photosynthesis and starch storage

periderm

> outermost covering of woody stems; consists of the cork cambium, cork cells, and the phelloderm

pith

ground tissue found towards the interior of the vascular tissue in a stem or root

primary growth
growth resulting in an increase in length of the stem and the root; caused by cell division in the shoot or root apical meristem

rhizome
modified underground stem that grows horizontally to the soil surface and has nodes and internodes

runner
stolon that runs above the ground and produces new clone plants at nodes

sclerenchyma cell
plant cell that has thick secondary walls and provides structural support; usually dead at maturity

secondary growth
growth resulting in an increase in thickness or girth; caused by the lateral meristem and cork cambium

sieve-tube cell
phloem cell arranged end to end to form a sieve tube that transports organic substances such as sugars and amino acids

stolon
modified stem that runs parallel to the ground and can give rise to new plants at the nodes

tendril
modified stem consisting of slender, twining strands used for support or climbing

thorn
modified stem branch appearing as a sharp outgrowth that protects the plant

tracheid
>   xylem cell with thick secondary walls that helps transport water

trichome
>   hair-like structure on the epidermal surface

tuber
>   modified underground stem adapted for starch storage; has many adventitious buds

vessel element
>   xylem cell that is shorter than a tracheid and has thinner walls

Roots
By the end of this section, you will be able to:

- Identify the two types of root systems
- Describe the three zones of the root tip and summarize the role of each zone in root growth
- Describe the structure of the root
- List and describe examples of modified roots

The roots of seed plants have three major functions: anchoring the plant to the soil, absorbing water and minerals and transporting them upwards, and storing the products of photosynthesis. Some roots are modified to absorb moisture and exchange gases. Most roots are underground. Some plants, however, also have **adventitious roots**, which emerge above the ground from the shoot.

Types of Root Systems

Root systems are mainly of two types ([link]). Dicots have a tap root system, while monocots have a fibrous root system. A **tap root system** has a main root that grows down vertically, and from which many smaller lateral roots arise. Dandelions are a good example; their tap roots usually break off when trying to pull these weeds, and they can regrow another shoot from the remaining root). A tap root system penetrates deep into the soil. In contrast, a **fibrous root system** is located closer to the soil surface, and forms a dense network of roots that also helps prevent soil erosion (lawn grasses are a good example, as are wheat, rice, and corn). Some plants have a combination of tap roots and fibrous roots. Plants that grow in dry areas often have deep root systems, whereas plants growing in areas with abundant water are likely to have shallower root systems.

(a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots. (credit b: modification of work by "Austen Squarepants"/Flickr)

Root Growth and Anatomy

Root growth begins with seed germination. When the plant embryo emerges from the seed, the radicle of the embryo forms the root system. The tip of the root is protected by the **root cap**, a structure exclusive to roots and unlike any other plant structure. The root cap is continuously replaced because it gets damaged easily as the root pushes through soil. The root tip can be divided into three zones: a zone of cell division, a zone of elongation, and a zone of maturation and differentiation ([link]). The zone of cell division is closest to the root tip; it is made up of the actively dividing cells of the root meristem. The zone of elongation is where the newly formed cells increase in length, thereby lengthening the root. Beginning at the first root hair is the zone of cell maturation where the root

cells begin to differentiate into special cell types. All three zones are in the first centimeter or so of the root tip.
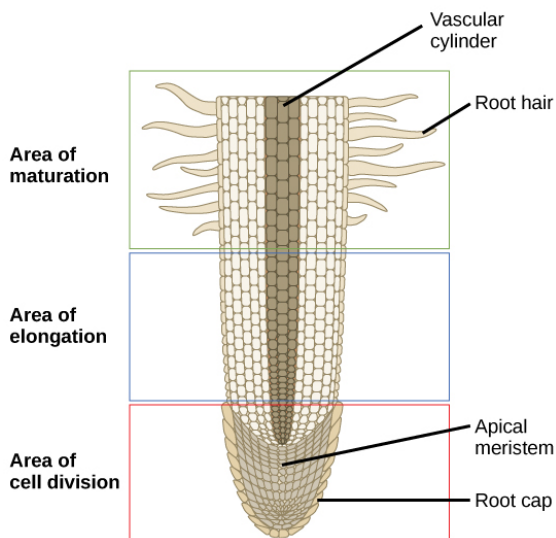
A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem.

The root has an outer layer of cells called the epidermis, which surrounds areas of ground tissue and vascular tissue. The epidermis provides protection and helps in absorption. **Root hairs**, which are extensions of root epidermal cells, increase the surface area of the root, greatly contributing to the absorption of water and minerals.

Inside the root, the ground tissue forms two regions: the cortex and the pith ([link]). Compared to stems, roots have lots of cortex and little pith. Both regions include cells that store photosynthetic products. The cortex is between the epidermis and the vascular tissue, whereas the pith lies between the vascular tissue and the center of the root.
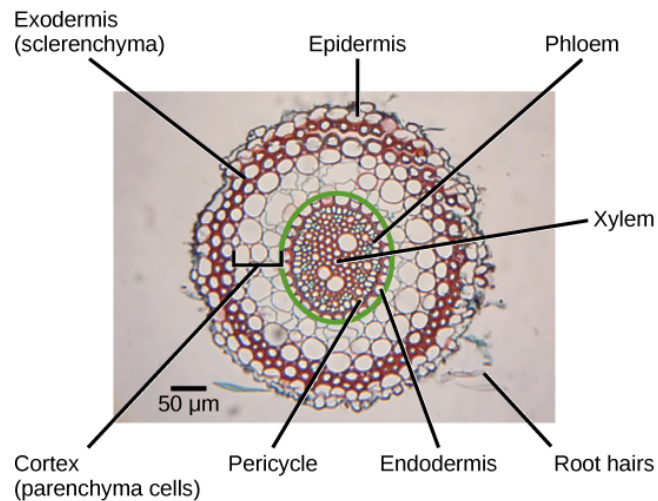
Staining reveals different cell types in this light micrograph of a wheat (*Triticum*) root cross section. Sclerenchyma cells of the exodermis and xylem cells stain red, and phloem cells stain blue. Other cell types stain black. The stele, or vascular tissue, is the area inside endodermis (indicated by a green ring). Root hairs are visible outside the epidermis. (credit: scale-bar data from Matt Russell)

The vascular tissue in the root is arranged in the inner portion of the root, which is called the **stele** ([link]). A layer of cells known as the **endodermis** separates the stele from the ground tissue in the outer portion of the root. The endodermis is exclusive to roots, and serves as a checkpoint for materials entering the root's vascular system. A waxy substance called suberin is present on the walls of the endodermal cells. This waxy region, known as the **Casparian strip**, forces water and solutes to cross the plasma membranes of endodermal cells instead of slipping between the cells. This ensures that only materials required by the root pass through the endodermis, while toxic substances and pathogens are generally excluded.

The outermost cell layer of the root's vascular tissue is the **pericycle**, an area that can give rise to lateral roots. In dicot roots, the xylem and phloem of the stele are arranged alternately in an X shape, whereas in monocot roots, the vascular tissue is arranged in a ring around the pith.
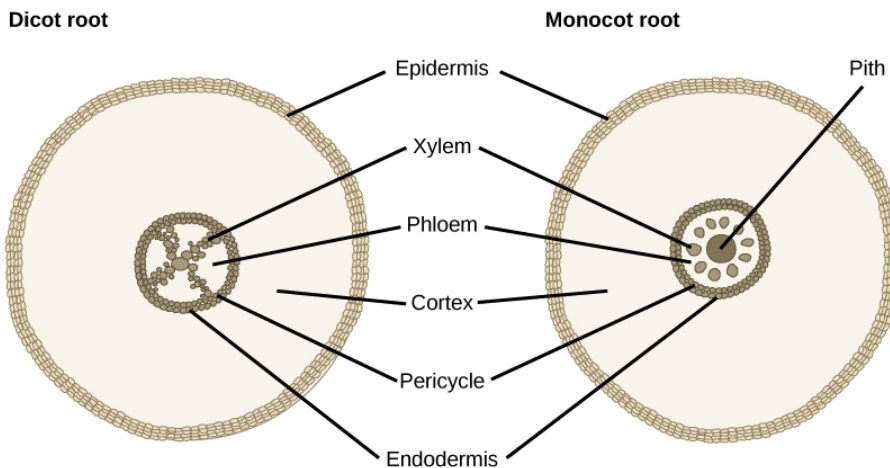
In (left) typical dicots, the vascular tissue forms an X shape in the center of the root. In (right) typical monocots, the phloem cells and the larger xylem cells form a characteristic ring around the central pith.

Root Modifications

Root structures may be modified for specific purposes. For example, some roots are bulbous and store starch. Aerial roots and prop roots are two forms of aboveground roots that provide additional support to anchor the plant. Tap roots, such as carrots, turnips, and beets, are examples of roots that are modified for food storage ([link]).

Many vegetables are modified roots.

Epiphytic roots enable a plant to grow on another plant. For example, the epiphytic roots of orchids develop a spongy tissue to absorb moisture. The banyan tree (*Ficus* sp.) begins as an epiphyte, germinating in the branches of a host tree; aerial roots develop from the branches and eventually reach the ground, providing additional support ([link]). In screwpine (*Pandanus* sp.), a palm-like tree that grows in sandy tropical soils, aboveground prop roots develop from the nodes to provide additional support.

(a)

(b)

The (a) banyan tree, also known as the strangler fig, begins life as an epiphyte in a host tree. Aerial roots extend to the ground and support the growing plant,

which eventually strangles the host tree. The (b) screwpine develops aboveground roots that help support the plant in sandy soils. (credit a: modification of work by "psyberartist"/Flickr; credit b: modification of work by David Eikhoff)

Section Summary

Roots help to anchor a plant, absorb water and minerals, and serve as storage sites for food. Taproots and fibrous roots are the two main types of root systems. In a taproot system, a main root grows vertically downward with a few lateral roots. Fibrous root systems arise at the base of the stem, where a cluster of roots forms a dense network that is shallower than a taproot. The growing root tip is protected by a root cap. The root tip has three main zones: a zone of cell division (cells are actively dividing), a zone of elongation (cells increase in length), and a zone of maturation (cells differentiate to form different kinds of cells). Root vascular tissue conducts water, minerals, and sugars. In some habitats, the roots of certain plants may be modified to form aerial roots or epiphytic roots.

Review Questions

Exercise:

Problem:

Roots that enable a plant to grow on another plant are called _____.

    a. epiphytic roots
    b. prop roots
    c. adventitious roots
    d. aerial roots

Solution:

A

Exercise:

Problem: The _____ forces selective uptake of minerals in the root.

    a. pericycle
    b. epidermis
    c. endodermis
    d. root cap

Solution:

C

Exercise:

Problem:

Newly-formed root cells begin to form different cell types in the _____.

    a. zone of elongation
    b. zone of maturation
    c. root meristem
    d. zone of cell division

Solution:

B

Free Response

Exercise:

Problem:

Compare a tap root system with a fibrous root system. For each type, name a plant that provides a food in the human diet. Which type of root system is found in monocots? Which type of root system is found in dicots?

Solution:

A tap root system has a single main root that grows down. A fibrous root system forms a dense network of roots that is closer to the soil surface. An example of a tap root system is a carrot. Grasses such as wheat, rice, and corn are examples of fibrous root systems. Fibrous root systems are found in monocots; tap root systems are found in dicots.

Exercise:

Problem: What might happen to a root if the pericycle disappeared?

Solution:

The root would not be able to produce lateral roots.

Glossary

adventitious root
> aboveground root that arises from a plant part other than the radicle of the plant embryo

Casparian strip
> waxy coating that forces water to cross endodermal plasma membranes before entering the vascular cylinder, instead of moving between endodermal cells

endodermis

layer of cells in the root that forms a selective barrier between the ground tissue and the vascular tissue, allowing water and minerals to enter the root while excluding toxins and pathogens

fibrous root system

type of root system in which the roots arise from the base of the stem in a cluster, forming a dense network of roots; found in monocots

pericycle

outer boundary of the stele from which lateral roots can arise

root cap

protective cells covering the tip of the growing root

root hair

hair-like structure that is an extension of epidermal cells; increases the root surface area and aids in absorption of water and minerals

stele

inner portion of the root containing the vascular tissue; surrounded by the endodermis

tap root system

type of root system with a main root that grows vertically with few lateral roots; found in dicots

Leaves
By the end of this section, you will be able to:

- Identify the parts of a typical leaf
- Describe the internal structure and function of a leaf
- Compare and contrast simple leaves and compound leaves
- List and describe examples of modified leaves

Leaves are the main sites for photosynthesis: the process by which plants synthesize food. Most leaves are usually green, due to the presence of chlorophyll in the leaf cells. However, some leaves may have different colors, caused by other plant pigments that mask the green chlorophyll.

The thickness, shape, and size of leaves are adapted to the environment. Each variation helps a plant species maximize its chances of survival in a particular habitat. Usually, the leaves of plants growing in tropical rainforests have larger surface areas than those of plants growing in deserts or very cold conditions, which are likely to have a smaller surface area to minimize water loss.

Structure of a Typical Leaf

Each leaf typically has a leaf blade called the **lamina**, which is also the widest part of the leaf. Some leaves are attached to the plant stem by a **petiole**. Leaves that do not have a petiole and are directly attached to the plant stem are called **sessile** leaves. Small green appendages usually found at the base of the petiole are known as **stipules**. Most leaves have a midrib, which travels the length of the leaf and branches to each side to produce veins of vascular tissue. The edge of the leaf is called the margin. [link] shows the structure of a typical eudicot leaf.
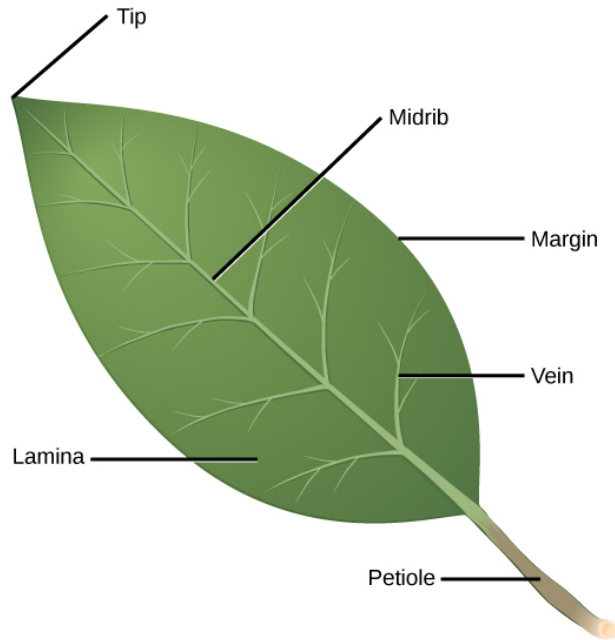
Deceptively simple in appearance, a leaf is a highly efficient structure.

Within each leaf, the vascular tissue forms veins. The arrangement of veins in a leaf is called the **venation** pattern. Monocots and dicots differ in their patterns of venation ([link]). Monocots have parallel venation; the veins run in straight lines across the length of the leaf without converging at a point. In dicots, however, the veins of the leaf have a net-like appearance, forming a pattern known as reticulate venation. One extant plant, the *Ginkgo biloba*, has dichotomous venation where the veins fork.
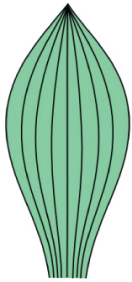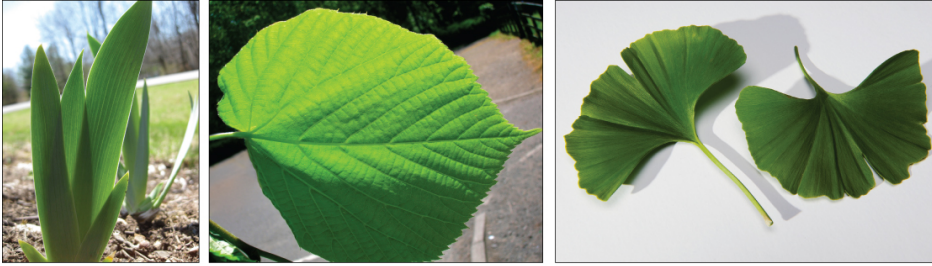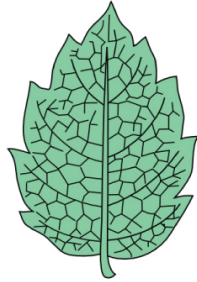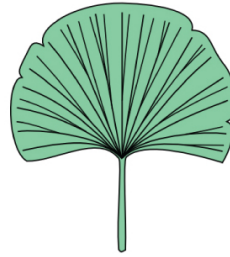
(a) Tulip (*Tulipa*), a monocot, has leaves with parallel venation. The netlike venation in this (b) linden (*Tilia cordata*) leaf distinguishes it as a dicot. The (c) *Ginkgo biloba* tree has dichotomous venation. (credit a photo: modification of work by "Drewboy64"/Wikimedia Commons; credit b photo: modification of work by Roger Griffith; credit c photo: modification of work by "geishaboy500"/Flickr; credit abc illustrations: modification of work by Agnieszka Kwiecień)

Leaf Arrangement

The arrangement of leaves on a stem is known as **phyllotaxy**. The number and placement of a plant's leaves will vary depending on the species, with each species exhibiting a characteristic leaf arrangement. Leaves are classified as either alternate, spiral, or opposite. Plants that have only one leaf per node have leaves that are said to be either alternate—meaning the leaves alternate on each side of the stem in a flat plane—or spiral, meaning the leaves are arrayed in a spiral along the stem. In an opposite leaf arrangement, two leaves arise at the same point, with the leaves connecting

opposite each other along the branch. If there are three or more leaves connected at a node, the leaf arrangement is classified as **whorled**.

Leaf Form

Leaves may be simple or compound ([link]). In a **simple leaf**, the blade is either completely undivided—as in the banana leaf—or it has lobes, but the separation does not reach the midrib, as in the maple leaf. In a **compound leaf**, the leaf blade is completely divided, forming leaflets, as in the locust tree. Each leaflet may have its own stalk, but is attached to the rachis. A **palmately compound leaf** resembles the palm of a hand, with leaflets radiating outwards from one point Examples include the leaves of poison ivy, the buckeye tree, or the familiar houseplant *Schefflera* sp. (common name "umbrella plant"). **Pinnately compound leaves** take their name from their feather-like appearance; the leaflets are arranged along the midrib, as in rose leaves (*Rosa* sp.), or the leaves of hickory, pecan, ash, or walnut trees.

(a) Simple

(b) Palmately compound

(c) Pinnately compound

(d) Doubly compound

Leaves may be simple or compound. In simple leaves, the lamina is continuous. The (a) banana plant (*Musa* sp.) has simple leaves. In compound leaves, the lamina is separated into leaflets. Compound leaves may be palmate or pinnate. In (b) palmately compound leaves, such as those of the horse chestnut (*Aesculus hippocastanum*), the leaflets branch from the petiole. In (c) pinnately compound leaves, the leaflets branch from the midrib, as on a scrub hickory (*Carya floridana*). The (d) honey locust has double compound leaves, in which leaflets branch from the veins. (credit a: modification of work by "BazzaDaRambler"/Flickr; credit b: modification of work by Roberto Verzo; credit c: modification of work by Eric Dion; credit d: modification of work by Valerie Lykes)

Leaf Structure and Function

The outermost layer of the leaf is the epidermis; it is present on both sides of the leaf and is called the upper and lower epidermis, respectively. Botanists call the upper side the adaxial surface (or adaxis) and the lower side the abaxial surface (or abaxis). The epidermis helps in the regulation of gas exchange. It contains stomata ([link]): openings through which the exchange of gases takes place. Two guard cells surround each stoma, regulating its opening and closing.
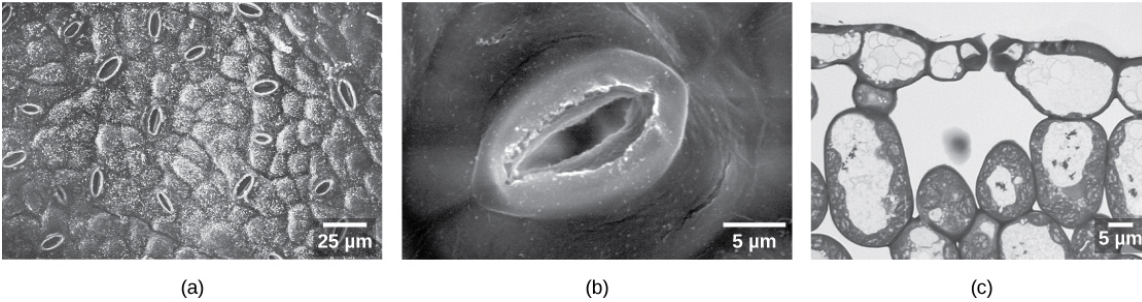
Visualized at 500x with a scanning electron microscope, several stomata are clearly visible on (a) the surface of this sumac (*Rhus glabra*) leaf. At 5,000x magnification, the guard cells of (b) a single stoma from lyre-leaved sand cress (*Arabidopsis lyrata)* have the appearance of lips that surround the opening. In this (c) light micrograph cross-section of an *A. lyrata* leaf, the guard cell pair is visible along with the large, sub-stomatal air space in the leaf. (credit: modification of work by Robert R. Wise; part c scale-bar data from Matt Russell)

The epidermis is usually one cell layer thick; however, in plants that grow in very hot or very cold conditions, the epidermis may be several layers thick to protect against excessive water loss from transpiration. A waxy layer known as the **cuticle** covers the leaves of all plant species. The cuticle reduces the rate of water loss from the leaf surface. Other leaves may have small hairs (trichomes) on the leaf surface. Trichomes help to deter herbivory by restricting insect movements, or by storing toxic or bad-tasting compounds; they can also reduce the rate of transpiration by blocking air flow across the leaf surface ([link]).
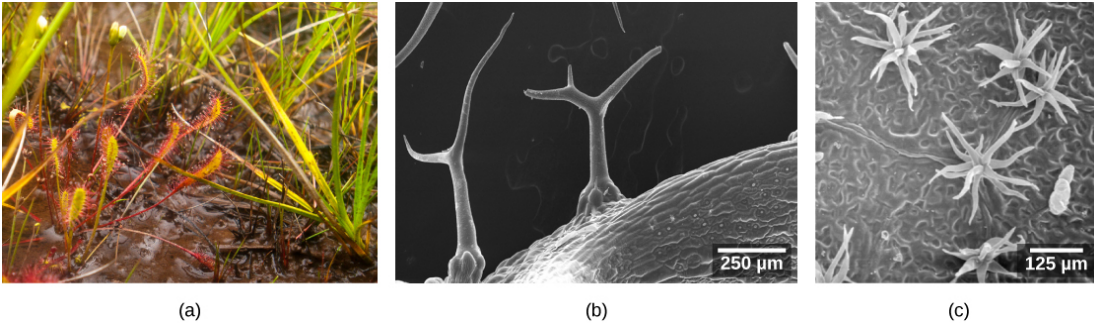
Trichomes give leaves a fuzzy appearance as in this (a) sundew (*Drosera* sp.). Leaf trichomes include (b) branched trichomes on the leaf of *Arabidopsis lyrata* and (c) multibranched trichomes on a mature *Quercus marilandica* leaf. (credit a: John Freeland; credit b, c: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Below the epidermis of dicot leaves are layers of cells known as the mesophyll, or "middle leaf." The mesophyll of most leaves typically contains two arrangements of parenchyma cells: the palisade parenchyma and spongy parenchyma ([link]). The palisade parenchyma (also called the palisade mesophyll) has column-shaped, tightly packed cells, and may be present in one, two, or three layers. Below the palisade parenchyma are loosely arranged cells of an irregular shape. These are the cells of the spongy parenchyma (or spongy mesophyll). The air space found between the spongy parenchyma cells allows gaseous exchange between the leaf and the outside atmosphere through the stomata. In aquatic plants, the intercellular spaces in the spongy parenchyma help the leaf float. Both layers of the mesophyll contain many chloroplasts. Guard cells are the only epidermal cells to contain chloroplasts.

(a)

200 μm
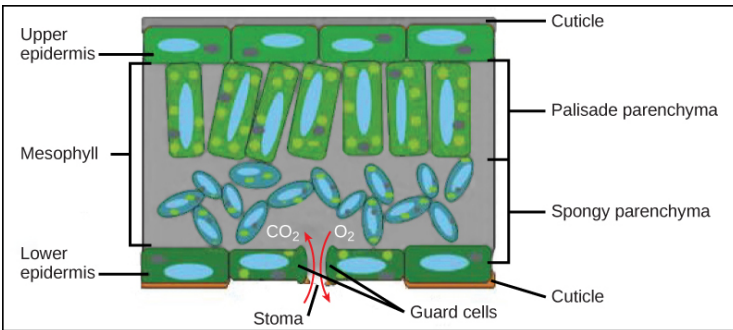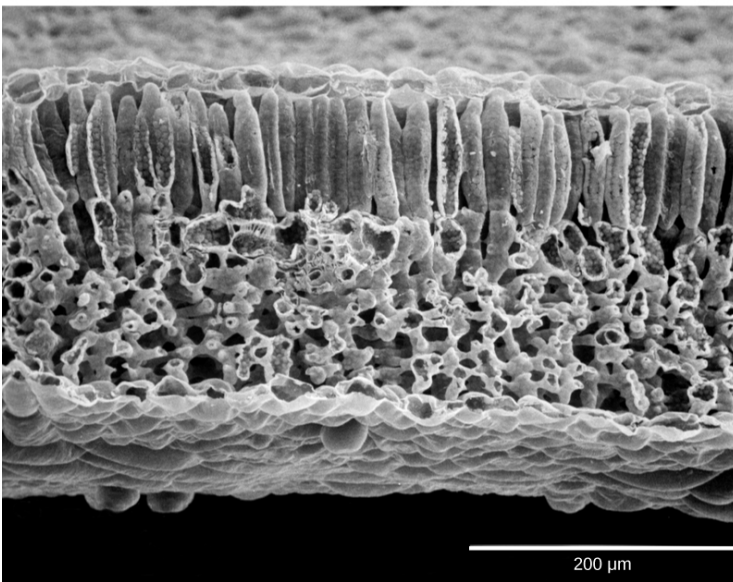
(b)

In the (a) leaf drawing, the central mesophyll is sandwiched between an upper and lower epidermis. The mesophyll has two layers: an upper palisade layer comprised of tightly packed, columnar cells, and a lower spongy layer, comprised of loosely packed, irregularly shaped cells. Stomata on the leaf underside allow gas exchange. A waxy cuticle covers all aerial surfaces of land plants to minimize water loss. These leaf layers are clearly visible in the (b) scanning electron micrograph. The numerous small bumps

in the palisade parenchyma cells are chloroplasts. Chloroplasts are also present in the spongy parenchyma, but are not as obvious. The bumps protruding from the lower surface of the leave are glandular trichomes, which differ in structure from the stalked trichomes in [link]. (credit b: modification of work by Robert R. Wise)

Like the stem, the leaf contains vascular bundles composed of xylem and phloem ([link]). The xylem consists of tracheids and vessels, which transport water and minerals to the leaves. The phloem transports the photosynthetic products from the leaf to the other parts of the plant. A single vascular bundle, no matter how large or small, always contains both xylem and phloem tissues.
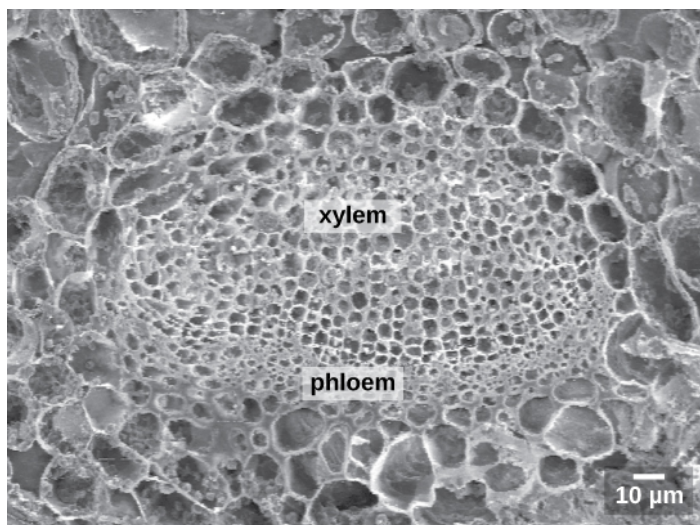
This scanning electron micrograph shows xylem and phloem in the leaf vascular bundle from the lyre-leaved sand cress (*Arabidopsis lyrata*).

(credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Leaf Adaptations

Coniferous plant species that thrive in cold environments, like spruce, fir, and pine, have leaves that are reduced in size and needle-like in appearance. These needle-like leaves have sunken stomata and a smaller surface area: two attributes that aid in reducing water loss. In hot climates, plants such as cacti have leaves that are reduced to spines, which in combination with their succulent stems, help to conserve water. Many aquatic plants have leaves with wide lamina that can float on the surface of the water, and a thick waxy cuticle on the leaf surface that repels water.

Note:
Link to Learning

Watch "The Pale Pitcher Plant" episode of the video series *Plants Are Cool, Too,* a Botanical Society of America video about a carnivorous plant species found in Louisiana.

Note:
Evolution Connection
Plant Adaptations in Resource-Deficient Environments

Roots, stems, and leaves are structured to ensure that a plant can obtain the required sunlight, water, soil nutrients, and oxygen resources. Some remarkable adaptations have evolved to enable plant species to thrive in less than ideal habitats, where one or more of these resources is in short supply.

In tropical rainforests, light is often scarce, since many trees and plants grow close together and block much of the sunlight from reaching the forest floor. Many tropical plant species have exceptionally broad leaves to maximize the capture of sunlight. Other species are epiphytes: plants that grow on other plants that serve as a physical support. Such plants are able to grow high up in the canopy atop the branches of other trees, where sunlight is more plentiful. Epiphytes live on rain and minerals collected in the branches and leaves of the supporting plant. Bromeliads (members of the pineapple family), ferns, and orchids are examples of tropical epiphytes ([link]). Many epiphytes have specialized tissues that enable them to efficiently capture and store water.

One of the most well known bromeliads is Spanish moss (*Tillandsia usneoides*), seen here in an oak tree. (credit: Kristine Paulus)

Some plants have special adaptations that help them to survive in nutrient-poor environments. Carnivorous plants, such as the Venus flytrap and the pitcher plant ([link]), grow in bogs where the soil is low in nitrogen. In these plants, leaves are modified to capture insects. The insect-capturing leaves may have evolved to provide these plants with a supplementary source of much-needed nitrogen.

(a)   (b)

The (a) Venus flytrap has modified leaves that can capture insects. When an unlucky insect touches the trigger hairs inside the leaf, the trap suddenly closes. The opening of the (b) pitcher plant is lined with a slippery wax. Insects crawling on the lip slip and fall into a pool of water in the bottom of the pitcher, where they are digested by bacteria. The plant then absorbs the smaller molecules. (credit a: modification of work by Peter Shanks; credit b: modification of work by Tim Mansfield)

Many swamp plants have adaptations that enable them to thrive in wet areas, where their roots grow submerged underwater. In these aquatic areas, the soil is unstable and little oxygen is available to reach the roots. Trees such as mangroves (*Rhizophora* sp.) growing in coastal waters produce aboveground roots that help support the tree ([link]). Some species of mangroves, as well as cypress trees, have pneumatophores: upward-

growing roots containing pores and pockets of tissue specialized for gas exchange. Wild rice is an aquatic plant with large air spaces in the root cortex. The air-filled tissue—called aerenchyma—provides a path for oxygen to diffuse down to the root tips, which are embedded in oxygen-poor bottom sediments.
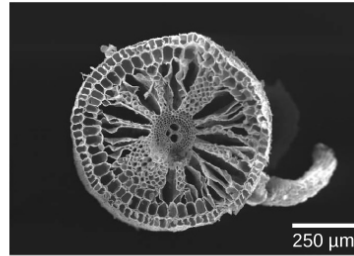
(a) (b) (c)

The branches of (a) mangrove trees develop aerial roots, which descend to the ground and help to anchor the trees. (b) Cypress trees and some mangrove species have upward-growing roots called pneumatophores that are involved in gas exchange. Aquatic plants such as (c) wild rice have large spaces in the root cortex called aerenchyma, visualized here using scanning electron microscopy. (credit a: modification of work by Roberto Verzo; credit b: modification of work by Duane Burdick; credit c: modification of work by Robert R. Wise)

Note:
Link to Learning

Watch *Venus Flytraps: Jaws of Death*, an extraordinary BBC close-up of the Venus flytrap in action.

Section Summary

Leaves are the main site of photosynthesis. A typical leaf consists of a lamina (the broad part of the leaf, also called the blade) and a petiole (the stalk that attaches the leaf to a stem). The arrangement of leaves on a stem, known as phyllotaxy, enables maximum exposure to sunlight. Each plant species has a characteristic leaf arrangement and form. The pattern of leaf arrangement may be alternate, opposite, or spiral, while leaf form may be simple or compound. Leaf tissue consists of the epidermis, which forms the outermost cell layer, and mesophyll and vascular tissue, which make up the inner portion of the leaf. In some plant species, leaf form is modified to form structures such as tendrils, spines, bud scales, and needles.

Review Questions

Exercise:

Problem: The stalk of a leaf is known as the _____.

   a. petiole
   b. lamina
   c. stipule
   d. rachis

Solution:

A

Exercise:

Problem: Leaflets are a characteristic of _____ leaves.

a. alternate
b. whorled
c. compound
d. opposite

Solution:

C

Exercise:

Problem: Cells of the _____ contain chloroplasts.

a. epidermis
b. vascular tissue
c. stomata
d. mesophyll

Solution:

D

Exercise:

Problem:

Which of the following is most likely to be found in a desert environment?

a. broad leaves to capture sunlight
b. spines instead of leaves
c. needle-like leaves
d. wide, flat leaves that can float

Solution:

B

Free Response

Exercise:

Problem:

How do dicots differ from monocots in terms of leaf structure?

Solution:

Monocots have leaves with parallel venation, and dicots have leaves with reticulate, net-like venation.

Exercise:

Problem:

Describe an example of a plant with leaves that are adapted to cold temperatures.

Solution:

Conifers such as spruce, fir, and pine have needle-shaped leaves with sunken stomata, helping to reduce water loss.

Glossary

compound leaf
> leaf in which the leaf blade is subdivided to form leaflets, all attached to the midrib

cuticle
> waxy protective layer on the leaf surface

lamina
> leaf blade

palmately compound leaf
    leaf type with leaflets that emerge from a point, resembling the palm of
    a hand

petiole
    stalk of the leaf

phyllotaxy
    arrangement of leaves on a stem

pinnately compound leaf
    leaf type with a divided leaf blade consisting of leaflets arranged on
    both sides of the midrib

sessile
    leaf without a petiole that is attached directly to the plant stem

simple leaf
    leaf type in which the lamina is completely undivided or merely lobed

stipule
    small green structure found on either side of the leaf stalk or petiole

venation
    pattern of veins in a leaf; may be parallel (as in monocots), reticulate
    (as in dicots), or dichotomous (as in *Gingko biloba*)

whorled
    pattern of leaf arrangement in which three or more leaves are
    connected at a node

Transport of Water and Solutes in Plants
By the end of this section, you will be able to:

- Define water potential and explain how it is influenced by solutes, pressure, gravity, and the matric potential
- Describe how water potential, evapotranspiration, and stomatal regulation influence how water is transported in plants
- Explain how photosynthates are transported in plants

The structure of plant roots, stems, and leaves facilitates the transport of water, nutrients, and photosynthates throughout the plant. The phloem and xylem are the main tissues responsible for this movement. Water potential, evapotranspiration, and stomatal regulation influence how water and nutrients are transported in plants. To understand how these processes work, we must first understand the energetics of water potential.

Water Potential

Plants are phenomenal hydraulic engineers. Using only the basic laws of physics and the simple manipulation of potential energy, plants can move water to the top of a 116-meter-tall tree ([link]**a**). Plants can also use hydraulics to generate enough force to split rocks and buckle sidewalks ([link]**b**). Plants achieve this because of water potential.

(a)   (b)

With heights nearing 116 meters, (a) coastal redwoods (*Sequoia sempervirens*) are the tallest trees in the world. Plant roots can easily generate enough force to (b) buckle and break concrete sidewalks, much to the dismay of homeowners and city maintenance departments. (credit a: modification of work by Bernt Rostad; credit b: modification of work by Pedestrians Educating Drivers on Safety, Inc.)

Water potential is a measure of the potential energy in water. Plant physiologists are not interested in the energy in any one particular aqueous system, but are very interested in water movement between two systems. In practical terms, therefore, water potential is the difference in potential energy between a given water sample and pure water (at atmospheric pressure and ambient temperature). Water potential is denoted by the Greek letter ψ (*psi*) and is expressed in units of pressure (pressure is a form of energy) called **megapascals** (MPa). The potential of pure water ($\Psi_w^{pure\ H2O}$) is, by convenience of definition, designated a value of zero (even though pure water contains plenty of potential energy, that energy is ignored). Water potential values for the water in a plant root, stem, or leaf are therefore expressed relative to $\Psi_w^{pure\ H2O}$.

The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects. Water potential can be broken down into its individual components using the following equation:
Equation:

$$\Psi_{system} = \Psi_{total} = \Psi_s + \Psi_p + \Psi_g + \Psi_m$$

where Ψ_s, Ψ_p, Ψ_g, and Ψ_m refer to the solute, pressure, gravity, and matric potentials, respectively. "System" can refer to the water potential of the soil water (Ψ^{soil}), root water (Ψ^{root}), stem water (Ψ^{stem}), leaf water (Ψ^{leaf}) or the water in the atmosphere ($\Psi^{atmosphere}$): whichever aqueous system is under consideration. As the individual components change, they raise or lower the

total water potential of a system. When this happens, water moves to equilibrate, moving from the system or compartment with a higher water potential to the system or compartment with a lower water potential. This brings the difference in water potential between the two systems ($\Delta\Psi$) back to zero ($\Delta\Psi = 0$). Therefore, for water to move through the plant from the soil to the air (a process called transpiration), Ψ^{soil} must be $> \Psi^{root} > \Psi^{stem} > \Psi^{leaf} > \Psi^{atmosphere}$.

Water only moves in response to $\Delta\Psi$, not in response to the individual components. However, because the individual components influence the total Ψ_{system}, by manipulating the individual components (especially Ψ_s), a plant can control water movement.

Solute Potential

Solute potential (Ψ_s), also called osmotic potential, is negative in a plant cell and zero in distilled water. Typical values for cell cytoplasm are -0.5 to -1.0 MPa. Solutes reduce water potential (resulting in a negative Ψ_w) by consuming some of the potential energy available in the water. Solute molecules can dissolve in water because water molecules can bind to them via hydrogen bonds; a hydrophobic molecule like oil, which cannot bind to water, cannot go into solution. The energy in the hydrogen bonds between solute molecules and water is no longer available to do work in the system because it is tied up in the bond. In other words, the amount of available potential energy is reduced when solutes are added to an aqueous system. Thus, Ψ_s decreases with increasing solute concentration. Because Ψ_s is one of the four components of Ψ_{system} or Ψ_{total}, a decrease in Ψ_s will cause a decrease in Ψ_{total}. The internal water potential of a plant cell is more negative than pure water because of the cytoplasm's high solute content ([link]). Because of this difference in water potential water will move from the soil into a plant's root cells via the process of osmosis. This is why solute potential is sometimes called osmotic potential.

Plant cells can metabolically manipulate Ψ_s (and by extension, Ψ_{total}) by adding or removing solute molecules. Therefore, plants have control over Ψ_{total} via their ability to exert metabolic control over Ψ_s.

Note:

Adding solute to the right side lowers ψ_s, causing water to move to the right side of the tube.

Applying positive pressure to the left side increases ψ_p, causing water to move to the right side of the tube.

Applying negative pressure to the left side lowers ψ_p, causing water to move to the left side of the tube.
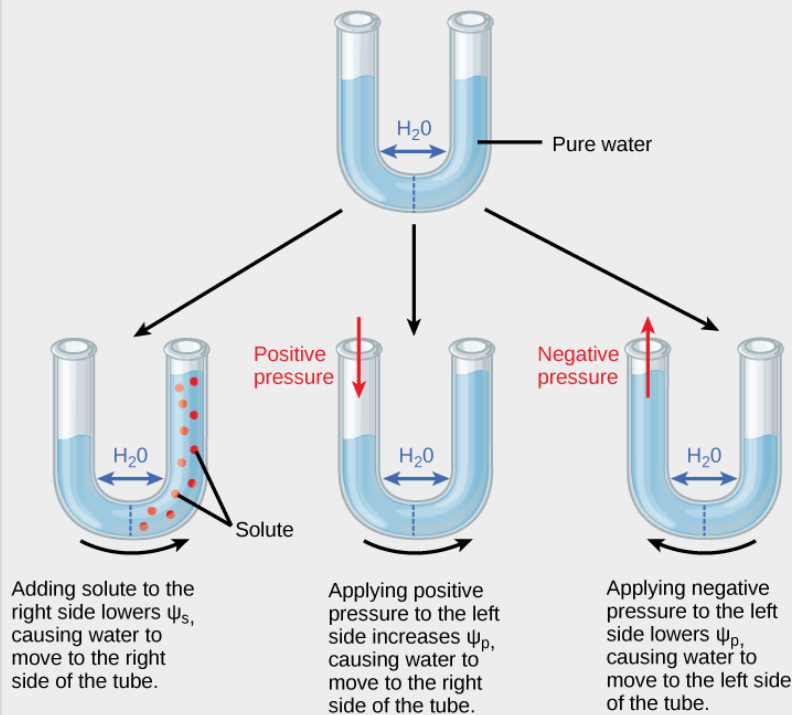
In this example with a semipermeable membrane between two aqueous systems, water will move from a region of higher to lower water potential until equilibrium is reached. Solutes (Ψ_s), pressure (Ψ_p), and gravity (Ψ_g) influence total water potential for each side of the tube ($\Psi_{total}^{\text{right or left}}$), and therefore, the difference between Ψ_{total} on each side ($\Delta\Psi$). (Ψ_m, the potential due to interaction of water with solid substrates, is ignored in this example because glass is not especially hydrophilic). Water moves in response to the difference in water potential between two systems (the left and right sides of the tube).

Positive water potential is placed on the left side of the tube by increasing Ψ_p such that the water level rises on the right side. Could you equalize the

water level on each side of the tube by adding solute, and if so, how?

Pressure Potential

Pressure potential (Ψ_p), also called turgor potential, may be positive or negative ([link]). Because pressure is an expression of energy, the higher the pressure, the more potential energy in a system, and vice versa. Therefore, a positive Ψp (compression) increases Ψ_{total}, and a negative Ψ_p (tension) decreases Ψ_{total}. Positive pressure inside cells is contained by the cell wall, producing turgor pressure. Pressure potentials are typically around 0.6–0.8 MPa, but can reach as high as 1.5 MPa in a well-watered plant. A Ψ_p of 1.5 MPa equates to 210 pounds per square inch (1.5 MPa x 140 lb in^{-2} MPa^{-1} = 210 lb/in^{-2}). As a comparison, most automobile tires are kept at a pressure of 30–34 psi. An example of the effect of turgor pressure is the wilting of leaves and their restoration after the plant has been watered ([link]). Water is lost from the leaves via transpiration (approaching Ψ_p = 0 MPa at the wilting point) and restored by uptake via the roots.

A plant can manipulate Ψ_p via its ability to manipulate Ψ_s and by the process of osmosis. If a plant cell increases the cytoplasmic solute concentration, Ψ_s will decline, Ψ_{total} will decline, the $\Delta\Psi$ between the cell and the surrounding tissue will decline, water will move into the cell by osmosis, and Ψ_p will increase. Ψ_p is also under indirect plant control via the opening and closing of stomata. Stomatal openings allow water to evaporate from the leaf, reducing Ψ_p and Ψ_{total} of the leaf and increasing ii between the water in the leaf and the petiole, thereby allowing water to flow from the petiole into the leaf.

(a)   (b)

When (a) total water potential (Ψ_{total}) is lower outside the cells than inside, water moves out of the cells and the plant wilts. When (b) the total water potential is higher outside the plant cells than inside, water moves into the cells, resulting in turgor pressure (Ψ_p) and keeping the plant erect. (credit: modification of work by Victor M. Vicente Selvas)

Gravity Potential

Gravity potential (Ψ_g) is always negative to zero in a plant with no height. It always removes or consumes potential energy from the system. The force of gravity pulls water downwards to the soil, reducing the total amount of potential energy in the water in the plant (Ψ_{total}). The taller the plant, the taller the water column, and the more influential Ψ_g becomes. On a cellular scale and in short plants, this effect is negligible and easily ignored. However, over the height of a tall tree like a giant coastal redwood, the gravitational pull of -0.1 MPa m^{-1} is equivalent to an extra 1 MPa of resistance that must be overcome for water to reach the leaves of the tallest trees. Plants are unable to manipulate Ψ_g.

Matric Potential

Matric potential (Ψ_m) is always negative to zero. In a dry system, it can be as low as –2 MPa in a dry seed, and it is zero in a water-saturated system. The binding of water to a matrix always removes or consumes potential energy from the system. Ψ_m is similar to solute potential because it involves tying up the energy in an aqueous system by forming hydrogen bonds between the water and some other component. However, in solute potential, the other components are soluble, hydrophilic solute molecules, whereas in Ψ_m, the other components are insoluble, hydrophilic molecules of the plant cell wall. Every plant cell has a cellulosic cell wall and the cellulose in the cell walls is hydrophilic, producing a matrix for adhesion of water: hence the name matric potential. Ψ_m is very large (negative) in dry tissues such as seeds or drought-affected soils. However, it quickly goes to zero as the seed takes up water or the soil hydrates. Ψ_m cannot be manipulated by the plant and is typically ignored in well-watered roots, stems, and leaves.

Movement of Water and Minerals in the Xylem

Solutes, pressure, gravity, and matric potential are all important for the transport of water in plants. Water moves from an area of higher total water potential (higher Gibbs free energy) to an area of lower total water potential. Gibbs free energy is the energy associated with a chemical reaction that can be used to do work. This is expressed as $\Delta\Psi$.

Transpiration is the loss of water from the plant through evaporation at the leaf surface. It is the main driver of water movement in the xylem. Transpiration is caused by the evaporation of water at the leaf–atmosphere interface; it creates negative pressure (tension) equivalent to –2 MPa at the leaf surface. This value varies greatly depending on the vapor pressure deficit, which can be negligible at high relative humidity (RH) and substantial at low RH. Water from the roots is pulled up by this tension. At night, when stomata shut and transpiration stops, the water is held in the stem and leaf by the adhesion of water to the cell walls of the xylem vessels and tracheids, and the cohesion of water molecules to each other. This is called the cohesion–tension theory of sap ascent.

Inside the leaf at the cellular level, water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to this leaf internal air space, and the water on the surface of the cells evaporates into the air spaces, decreasing the thin film on the surface of the mesophyll cells. This decrease creates a greater tension on the water in the mesophyll cells ([link]), thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Rings in the vessels maintain their tubular shape, much like the rings on a vacuum cleaner hose keep the hose open while it is under pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that can form via a process called cavitation. The formation of gas bubbles in xylem interrupts the continuous stream of water from the base to the top of the plant, causing a break termed an embolism in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water, and the more cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them non-functional.

Note:
Art Connection

Mesophyll cells
Xylem
Stoma

Transpiration draws water from the leaf.

Xylem

Cohesion and adhesion draw water up the xylem.

Root hairs
Soil particle
Water molecule
Xylem

Negative water potential draws water into the root.

Low

Atmosphere: ~–100 MPa

Leaf at tip of tree: ~–1.5 MPa

Water potential gradient

Stem:~–0.6 MPa

High

Root cells: ~–0.2 MPa
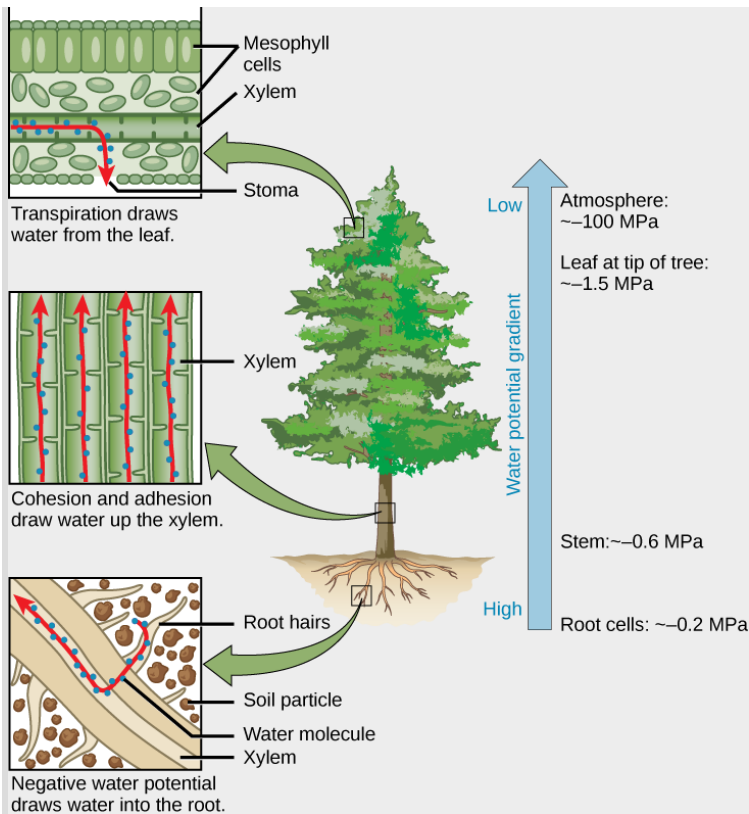
The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.

Which of the following statements is false?

a. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf.
b. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the phloem. Transpiration draws water from the leaf.
c. Water potential decreases from the roots to the top of the plant.
d. Water enters the plants through root hairs and exits through stoma.

Transpiration—the loss of water vapor to the atmosphere through stomata —is a passive process, meaning that metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in energy between the water in the soil and the water in the atmosphere. However, transpiration is tightly controlled.

Control of Transpiration

The atmosphere to which the leaf is exposed drives transpiration, but also causes massive water loss from the plant. Up to 90 percent of the water taken up by roots may be lost through transpiration.

Leaves are covered by a waxy **cuticle** on the outer surface that prevents the loss of water. Regulation of transpiration, therefore, is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells, which open and close in response to environmental cues such as light intensity and quality, leaf water status, and carbon dioxide concentrations. Stomata must open to allow air containing carbon dioxide and oxygen to diffuse into the leaf for photosynthesis and respiration. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between efficient photosynthesis and water loss.

Plants have evolved over time to adapt to their local environment and reduce transpiration([link]). Desert plant (xerophytes) and plants that grow on other plants (epiphytes) have limited access to water. Such plants usually have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (mesophytes). Aquatic plants (hydrophytes) also have their own set of anatomical and morphological leaf adaptations.

(a)

(b)

(c)

(d)

Plants are suited to their local environment. (a) Xerophytes, like this prickly pear cactus (*Opuntia sp.*) and (b) epiphytes such as this tropical *Aeschynanthus perrottetii* have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. (b) *A. perottetii* leaves have a waxy cuticle that prevents water loss. (c) Goldenrod (*Solidago sp.*) is a mesophyte, well suited for moderate environments. (d)

Xerophytes and epiphytes often have a thick covering of trichomes or of stomata that are sunken below the leaf's surface. Trichomes are specialized hair-like epidermal cells that secrete oils and substances. These adaptations impede air flow across the stomatal pore and reduce transpiration. Multiple epidermal layers are also commonly found in these types of plants.

Transportation of Photosynthates in the Phloem

Plants need an energy source to grow. In seeds and bulbs, food is stored in polymers (such as starch) that are converted by metabolic processes into sucrose for newly developing plants. Once green shoots and leaves are growing, plants are able to produce their own food by photosynthesizing. The products of photosynthesis are called photosynthates, which are usually in the form of simple sugars such as sucrose.

Structures that produce photosynthates for the growing plant are referred to as **sources**. Sugars produced in sources, such as leaves, need to be delivered to growing parts of the plant via the phloem in a process called **translocation**. The points of sugar delivery, such as roots, young shoots, and developing seeds, are called **sinks**. Seeds, tubers, and bulbs can be either a source or a sink, depending on the plant's stage of development and the season.

The products from the source are usually translocated to the nearest sink through the phloem. For example, the highest leaves will send

photosynthates upward to the growing shoot tip, whereas lower leaves will direct photosynthates downward to the roots. Intermediate leaves will send products in both directions, unlike the flow in the xylem, which is always unidirectional (soil to leaf to atmosphere). The pattern of photosynthate flow changes as the plant grows and develops. Photosynthates are directed primarily to the roots early on, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to tubers for storage.

Translocation: Transport from Source to Sink

Photosynthates, such as sucrose, are produced in the mesophyll cells of photosynthesizing leaves. From there they are translocated through the phloem to where they are used or stored. Mesophyll cells are connected by cytoplasmic channels called plasmodesmata. Photosynthates move through these channels to reach phloem sieve-tube elements (STEs) in the vascular bundles. From the mesophyll cells, the photosynthates are loaded into the phloem STEs. The sucrose is actively transported against its concentration gradient (a process requiring ATP) into the phloem cells using the electrochemical potential of the proton gradient. This is coupled to the uptake of sucrose with a carrier protein called the sucrose-H$^+$ symporter.

Phloem STEs have reduced cytoplasmic contents, and are connected by a sieve plate with pores that allow for pressure-driven bulk flow, or translocation, of phloem sap. Companion cells are associated with STEs. They assist with metabolic activities and produce energy for the STEs ([link]).
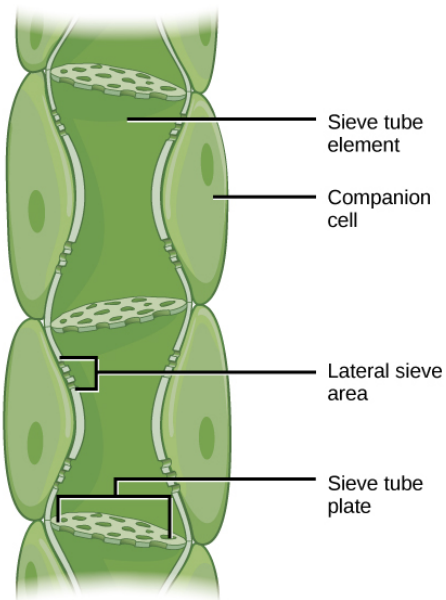
Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells.

Once in the phloem, the photosynthates are translocated to the closest sink. Phloem sap is an aqueous solution that contains up to 30 percent sugar, minerals, amino acids, and plant growth regulators. The high percentage of sugar decreases Ψ_S, which decreases the total water potential and causes

water to move by osmosis from the adjacent xylem into the phloem tubes, thereby increasing pressure. This increase in total water potential causes the bulk flow of phloem from source to sink ([link]). Sucrose concentration in the sink cells is lower than in the phloem STEs because the sink sucrose has been metabolized for growth, or converted to starch for storage or other polymers, such as cellulose, for structural integrity. Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Water diffuses from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.
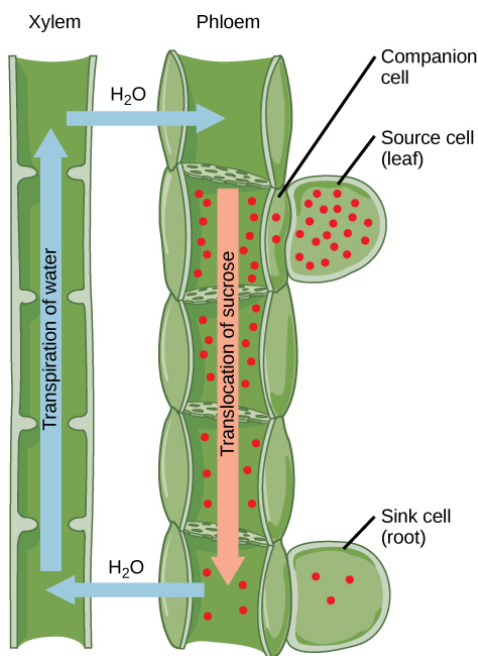
Sucrose is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem.

The resulting positive pressure forces the sucrose-water mixture down toward the roots, where sucrose is unloaded. Transpiration causes water to return to the leaves through the xylem vessels.

Section Summary

Water potential (Ψ) is a measure of the difference in potential energy between a water sample and pure water. The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and matric potential. Water potential and transpiration influence how water is transported through the xylem in plants. These processes are regulated by stomatal opening and closing. Photosynthates (mainly sucrose) move from sources to sinks through the plant's phloem. Sucrose is actively loaded into the sieve-tube elements of the phloem. The increased solute concentration causes water to move by osmosis from the xylem into the phloem. The positive pressure that is produced pushes water and solutes down the pressure gradient. The sucrose is unloaded into the sink, and the water returns to the xylem vessels.

Art Connections

Exercise:

Problem:

[link] Positive water potential is placed on the left side of the tube by increasing Ψ_p such that the water level rises on the right side. Could you equalize the water level on each side of the tube by adding solute, and if so, how?

Solution:

[link] Yes, you can equalize the water level by adding the solute to the left side of the tube such that water moves toward the left until the water levels are equal.

Exercise:

Problem: [link] Which of the following statements is false?

   a. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf.
   b. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the phloem. Transpiration draws water from the leaf.
   c. Water potential decreases from the roots to the top of the plant.
   d. Water enters the plants through root hairs and exits through stoma.

Solution:

[link] B.

Review Questions

Exercise:

Problem: When stomata open, what occurs?

   a. Water vapor is lost to the external environment, increasing the rate of transpiration.
   b. Water vapor is lost to the external environment, decreasing the rate of transpiration.

c. Water vapor enters the spaces in the mesophyll, increasing the rate of transpiration.

d. Water vapor enters the spaces in the mesophyll, increasing the rate of transpiration.

Solution:

A

Exercise:

Problem:

Which cells are responsible for the movement of photosynthates through a plant?

a. tracheids, vessel elements
b. tracheids, companion cells
c. vessel elements, companion cells
d. sieve-tube elements, companion cells

Solution:

D

Free Response

Exercise:

Problem:

The process of bulk flow transports fluids in a plant. Describe the two main bulk flow processes.

Solution:

The process of bulk flow moves water up the xylem and moves photosynthates (solutes) up and down the phloem.

Glossary

cuticle
    waxy covering on the outside of the leaf and stem that prevents the loss of water

megapascal (MPa)
    pressure units that measure water potential

sink
    growing parts of a plant, such as roots and young leaves, which require photosynthate

source
    organ that produces photosynthate for a plant

translocation
    mass transport of photosynthates from source to sink in vascular plants

transpiration
    loss of water vapor to the atmosphere through stomata

water potential (Ψ_w)
    the potential energy of a water solution per unit volume in relation to pure water at atmospheric pressure and ambient temperature

Plant Sensory Systems and Responses
By the end of this section, you will be able to:

- Describe how red and blue light affect plant growth and metabolic activities
- Discuss gravitropism
- Understand how hormones affect plant growth and development
- Describe thigmotropism, thigmonastism, and thigmogenesis
- Explain how plants defend themselves from predators and respond to wounds

Animals can respond to environmental factors by moving to a new location. Plants, however, are rooted in place and must respond to the surrounding environmental factors. Plants have sophisticated systems to detect and respond to light, gravity, temperature, and physical touch. Receptors sense environmental factors and relay the information to effector systems—often through intermediate chemical messengers—to bring about plant responses.

Plant Responses to Light

Plants have a number of sophisticated uses for light that go far beyond their ability to photosynthesize low-molecular-weight sugars using only carbon dioxide, light, and water. **Photomorphogenesis** is the growth and development of plants in response to light. It allows plants to optimize their use of light and space. **Photoperiodism** is the ability to use light to track time. Plants can tell the time of day and time of year by sensing and using various wavelengths of sunlight. **Phototropism** is a directional response that allows plants to grow towards, or even away from, light.

The sensing of light in the environment is important to plants; it can be crucial for competition and survival. The response of plants to light is mediated by different photoreceptors, which are comprised of a protein covalently bonded to a light-absorbing pigment called a **chromophore**. Together, the two are called a chromoprotein.

The red/far-red and violet-blue regions of the visible light spectrum trigger structural development in plants. Sensory photoreceptors absorb light in

these particular regions of the visible light spectrum because of the quality of light available in the daylight spectrum. In terrestrial habitats, light absorption by chlorophylls peaks in the blue and red regions of the spectrum. As light filters through the canopy and the blue and red wavelengths are absorbed, the spectrum shifts to the far-red end, shifting the plant community to those plants better adapted to respond to far-red light. Blue-light receptors allow plants to gauge the direction and abundance of sunlight, which is rich in blue–green emissions. Water absorbs red light, which makes the detection of blue light essential for algae and aquatic plants.

The Phytochrome System and the Red/Far-Red Response

The **phytochromes** are a family of chromoproteins with a linear tetrapyrrole chromophore, similar to the ringed tetrapyrrole light-absorbing head group of chlorophyll. Phytochromes have two photo-interconvertible forms: Pr and Pfr. Pr absorbs red light (~667 nm) and is immediately converted to Pfr. Pfr absorbs far-red light (~730 nm) and is quickly converted back to Pr. Absorption of red or far-red light causes a massive change to the shape of the chromophore, altering the conformation and activity of the phytochrome protein to which it is bound. Pfr is the physiologically active form of the protein; therefore, exposure to red light yields physiological activity. Exposure to far-red light inhibits phytochrome activity. Together, the two forms represent the phytochrome system ([link]).

The phytochrome system acts as a biological light switch. It monitors the level, intensity, duration, and color of environmental light. The effect of red light is reversible by immediately shining far-red light on the sample, which converts the chromoprotein to the inactive Pr form. Additionally, Pfr can slowly revert to Pr in the dark, or break down over time. In all instances, the physiological response induced by red light is reversed. The active form of phytochrome (Pfr) can directly activate other molecules in the cytoplasm, or it can be trafficked to the nucleus, where it directly activates or represses specific gene expression.

Once the phytochrome system evolved, plants adapted it to serve a variety of needs. Unfiltered, full sunlight contains much more red light than far-red light. Because chlorophyll absorbs strongly in the red region of the visible spectrum, but not in the far-red region, any plant in the shade of another plant on the forest floor will be exposed to red-depleted, far-red-enriched light. The preponderance of far-red light converts phytochrome in the shaded leaves to the Pr (inactive) form, slowing growth. The nearest non-shaded (or even less-shaded) areas on the forest floor have more red light; leaves exposed to these areas sense the red light, which activates the Pfr form and induces growth. In short, plant shoots use the phytochrome system to grow away from shade and towards light. Because competition for light is so fierce in a dense plant community, the evolutionary advantages of the phytochrome system are obvious.

In seeds, the phytochrome system is not used to determine direction and quality of light (shaded versus unshaded). Instead, is it used merely to determine if there is any light at all. This is especially important in species with very small seeds, such as lettuce. Because of their size, lettuce seeds have few food reserves. Their seedlings cannot grow for long before they run out of fuel. If they germinated even a centimeter under the soil surface, the seedling would never make it into the sunlight and would die. In the dark, phytochrome is in the Pr (inactive form) and the seed will not germinate; it will only germinate if exposed to light at the surface of the soil. Upon exposure to light, Pr is converted to Pfr and germination proceeds.
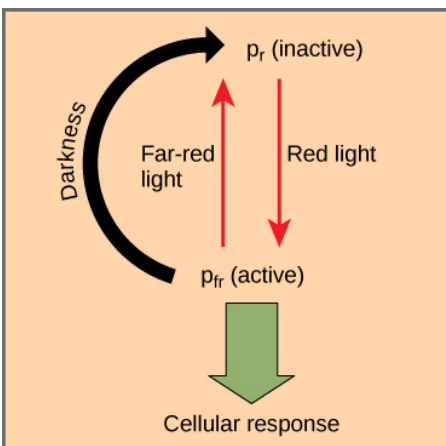
The biologically inactive form of phytochrome (Pr) is converted to the biologically active form Pfr under illumination with red light. Far-red light and darkness convert the molecule back to the inactive form.

Plants also use the phytochrome system to sense the change of season. Photoperiodism is a biological response to the timing and duration of day and night. It controls flowering, setting of winter buds, and vegetative growth. Detection of seasonal changes is crucial to plant survival. Although temperature and light intensity influence plant growth, they are not reliable indicators of season because they may vary from one year to the next. Day length is a better indicator of the time of year.

As stated above, unfiltered sunlight is rich in red light but deficient in far-red light. Therefore, at dawn, all the phytochrome molecules in a leaf quickly convert to the active Pfr form, and remain in that form until sunset. In the dark, the Pfr form takes hours to slowly revert back to the Pr form. If the night is long (as in winter), all of the Pfr form reverts. If the night is short (as in summer), a considerable amount of Pfr may remain at sunrise. By sensing the Pr/Pfr ratio at dawn, a plant can determine the length of the day/night cycle. In addition, leaves retain that information for several days, allowing a comparison between the length of the previous night and the preceding several nights. Shorter nights indicate springtime to the plant; when the nights become longer, autumn is approaching. This information, along with sensing temperature and water availability, allows plants to determine the time of the year and adjust their physiology accordingly. Short-day (long-night) plants use this information to flower in the late

summer and early fall, when nights exceed a critical length (often eight or fewer hours). Long-day (short-night) plants flower during the spring, when darkness is less than a critical length (often eight to 15 hours). Not all plants use the phytochrome system in this way. Flowering in day-neutral plants is not regulated by daylength.

Note:
Career Connection
Horticulturalist
The word "horticulturist" comes from the Latin words for garden (*hortus*) and culture (*cultura*). This career has been revolutionized by progress made in the understanding of plant responses to environmental stimuli. Growers of crops, fruit, vegetables, and flowers were previously constrained by having to time their sowing and harvesting according to the season. Now, horticulturists can manipulate plants to increase leaf, flower, or fruit production by understanding how environmental factors affect plant growth and development.
Greenhouse management is an essential component of a horticulturist's education. To lengthen the night, plants are covered with a blackout shade cloth. Long-day plants are irradiated with red light in winter to promote early flowering. For example, fluorescent (cool white) light high in blue wavelengths encourages leafy growth and is excellent for starting seedlings. Incandescent lamps (standard light bulbs) are rich in red light, and promote flowering in some plants. The timing of fruit ripening can be increased or delayed by applying plant hormones. Recently, considerable progress has been made in the development of plant breeds that are suited to different climates and resistant to pests and transportation damage. Both crop yield and quality have increased as a result of practical applications of the knowledge of plant responses to external stimuli and hormones. Horticulturists find employment in private and governmental laboratories, greenhouses, botanical gardens, and in the production or research fields. They improve crops by applying their knowledge of genetics and plant physiology. To prepare for a horticulture career, students take classes in botany, plant physiology, plant pathology, landscape design, and plant

breeding. To complement these traditional courses, horticulture majors add studies in economics, business, computer science, and communications.

The Blue Light Responses

Phototropism—the directional bending of a plant toward or away from a light source—is a response to blue wavelengths of light. Positive phototropism is growth towards a light source ([link]), while negative phototropism (also called skototropism) is growth away from light.

The aptly-named **phototropins** are protein-based receptors responsible for mediating the phototropic response. Like all plant photoreceptors, phototropins consist of a protein portion and a light-absorbing portion, called the chromophore. In phototropins, the chromophore is a covalently-bound molecule of flavin; hence, phototropins belong to a class of proteins called flavoproteins.

Other responses under the control of phototropins are leaf opening and closing, chloroplast movement, and the opening of stomata. However, of all responses controlled by phototropins, phototropism has been studied the longest and is the best understood.

In their 1880 treatise *The Power of Movements in Plants*, Charles Darwin and his son Francis first described phototropism as the bending of seedlings toward light. Darwin observed that light was perceived by the tip of the plant (the apical meristem), but that the response (bending) took place in a different part of the plant. They concluded that the signal had to travel from the apical meristem to the base of the plant.

Azure bluets (*Houstonia caerulea*) display a phototropic response by bending toward the light. (credit: Cory Zanker)

In 1913, Peter Boysen-Jensen demonstrated that a chemical signal produced in the plant tip was responsible for the bending at the base. He cut off the tip of a seedling, covered the cut section with a layer of gelatin, and then replaced the tip. The seedling bent toward the light when illuminated. However, when impermeable mica flakes were inserted between the tip and the cut base, the seedling did not bend. A refinement of the experiment showed that the signal traveled on the shaded side of the seedling. When the mica plate was inserted on the illuminated side, the plant did bend towards the light. Therefore, the chemical signal was a growth stimulant because the phototropic response involved faster cell elongation on the shaded side than on the illuminated side. We now know that as light passes through a plant stem, it is diffracted and generates phototropin activation across the stem. Most activation occurs on the lit side, causing the plant hormone indole acetic acid (IAA) to accumulate on the shaded side. Stem cells elongate under influence of IAA.

Cryptochromes are another class of blue-light absorbing photoreceptors that also contain a flavin-based chromophore. Cryptochromes set the plants

24-hour activity cycle, also know as its circadian rhythem, using blue light cues. There is some evidence that cryptochromes work together with phototropins to mediate the phototropic response.

Plant Responses to Gravity

Whether or not they germinate in the light or in total darkness, shoots usually sprout up from the ground, and roots grow downward into the ground. A plant laid on its side in the dark will send shoots upward when given enough time. Gravitropism ensures that roots grow into the soil and that shoots grow toward sunlight. Growth of the shoot apical tip upward is called **negative gravitropism**, whereas growth of the roots downward is called **positive gravitropism**.

Amyloplasts (also known as **statoliths**) are specialized plastids that contain starch granules and settle downward in response to gravity. Amyloplasts are found in shoots and in specialized cells of the root cap. When a plant is tilted, the statoliths drop to the new bottom cell wall. A few hours later, the shoot or root will show growth in the new vertical direction.

The mechanism that mediates gravitropism is reasonably well understood. When amyloplasts settle to the bottom of the gravity-sensing cells in the

root or shoot, they physically contact the endoplasmic reticulum (ER), causing the release of calcium ions from inside the ER. This calcium signaling in the cells causes polar transport of the plant hormone IAA to the bottom of the cell. In roots, a high concentration of IAA inhibits cell elongation. The effect slows growth on the lower side of the root, while cells develop normally on the upper side. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion, causing the shoot to grow up. After the shoot or root begin to grow vertically, the amyloplasts return to their normal position. Other hypotheses—involving the entire cell in the gravitropism effect—have been proposed to explain why some mutants that lack amyloplasts may still exhibit a weak gravitropic response.

Growth Responses

A plant's sensory response to external stimuli relies on chemical messengers (hormones). Plant hormones affect all aspects of plant life, from flowering to fruit setting and maturation, and from phototropism to leaf fall. Potentially every cell in a plant can produce plant hormones. They can act in their cell of origin or be transported to other portions of the plant body, with many plant responses involving the synergistic or antagonistic interaction of two or more hormones. In contrast, animal hormones are produced in specific glands and transported to a distant site for action, and they act alone.

Plant hormones are a group of unrelated chemical substances that affect plant morphogenesis. Five major plant hormones are traditionally described: auxins (particularly IAA), cytokinins, gibberellins, ethylene, and abscisic acid. In addition, other nutrients and environmental conditions can be characterized as growth factors.

Auxins

The term auxin is derived from the Greek word *auxein*, which means "to grow." **Auxins** are the main hormones responsible for cell elongation in

phototropism and gravitropism. They also control the differentiation of meristem into vascular tissue, and promote leaf development and arrangement. While many synthetic auxins are used as herbicides, IAA is the only naturally occurring auxin that shows physiological activity. Apical dominance—the inhibition of lateral bud formation—is triggered by auxins produced in the apical meristem. Flowering, fruit setting and ripening, and inhibition of **abscission** (leaf falling) are other plant responses under the direct or indirect control of auxins. Auxins also act as a relay for the effects of the blue light and red/far-red responses.

Commercial use of auxins is widespread in plant nurseries and for crop production. IAA is used as a rooting hormone to promote growth of adventitious roots on cuttings and detached leaves. Applying synthetic auxins to tomato plants in greenhouses promotes normal fruit development. Outdoor application of auxin promotes synchronization of fruit setting and dropping to coordinate the harvesting season. Fruits such as seedless cucumbers can be induced to set fruit by treating unfertilized plant flowers with auxins.

Cytokinins

The effect of cytokinins was first reported when it was found that adding the liquid endosperm of coconuts to developing plant embryos in culture stimulated their growth. The stimulating growth factor was found to be **cytokinin**, a hormone that promotes cytokinesis (cell division). Almost 200 naturally occurring or synthetic cytokinins are known to date. Cytokinins are most abundant in growing tissues, such as roots, embryos, and fruits, where cell division is occurring. Cytokinins are known to delay senescence in leaf tissues, promote mitosis, and stimulate differentiation of the meristem in shoots and roots. Many effects on plant development are under the influence of cytokinins, either in conjunction with auxin or another hormone. For example, apical dominance seems to result from a balance between auxins that inhibit lateral buds, and cytokinins that promote bushier growth.

Gibberellins

Gibberellins (GAs) are a group of about 125 closely related plant hormones that stimulate shoot elongation, seed germination, and fruit and flower maturation. GAs are synthesized in the root and stem apical meristems, young leaves, and seed embryos. In urban areas, GA antagonists are sometimes applied to trees under power lines to control growth and reduce the frequency of pruning.

GAs break dormancy (a state of inhibited growth and development) in the seeds of plants that require exposure to cold or light to germinate. Abscisic acid is a strong antagonist of GA action. Other effects of GAs include gender expression, seedless fruit development, and the delay of senescence in leaves and fruit. Seedless grapes are obtained through standard breeding methods and contain inconspicuous seeds that fail to develop. Because GAs are produced by the seeds, and because fruit development and stem elongation are under GA control, these varieties of grapes would normally produce small fruit in compact clusters. Maturing grapes are routinely treated with GA to promote larger fruit size, as well as looser bunches (longer stems), which reduces the instance of mildew infection ([link]).

In grapes, application of gibberellic acid increases the size of fruit and loosens clustering. (credit: Bob Nichols, USDA)

Abscisic Acid

The plant hormone **abscisic acid** (ABA) was first discovered as the agent that causes the abscission or dropping of cotton bolls. However, more recent studies indicate that ABA plays only a minor role in the abscission process. ABA accumulates as a response to stressful environmental conditions, such as dehydration, cold temperatures, or shortened day lengths. Its activity counters many of the growth-promoting effects of GAs and auxins. ABA inhibits stem elongation and induces dormancy in lateral buds.

ABA induces dormancy in seeds by blocking germination and promoting the synthesis of storage proteins. Plants adapted to temperate climates require a long period of cold temperature before seeds germinate. This mechanism protects young plants from sprouting too early during unseasonably warm weather in winter. As the hormone gradually breaks down over winter, the seed is released from dormancy and germinates when conditions are favorable in spring. Another effect of ABA is to promote the development of winter buds; it mediates the conversion of the apical meristem into a dormant bud. Low soil moisture causes an increase in ABA, which causes stomata to close, reducing water loss in winter buds.

Ethylene

Ethylene is associated with fruit ripening, flower wilting, and leaf fall. Ethylene is unusual because it is a volatile gas (C_2H_4). Hundreds of years ago, when gas street lamps were installed in city streets, trees that grew close to lamp posts developed twisted, thickened trunks and shed their leaves earlier than expected. These effects were caused by ethylene volatilizing from the lamps.

Aging tissues (especially senescing leaves) and nodes of stems produce ethylene. The best-known effect of the hormone, however, is the promotion of fruit ripening. Ethylene stimulates the conversion of starch and acids to sugars. Some people store unripe fruit, such as avocadoes, in a sealed paper bag to accelerate ripening; the gas released by the first fruit to mature will speed up the maturation of the remaining fruit. Ethylene also triggers leaf and fruit abscission, flower fading and dropping, and promotes germination in some cereals and sprouting of bulbs and potatoes.

Ethylene is widely used in agriculture. Commercial fruit growers control the timing of fruit ripening with application of the gas. Horticulturalists inhibit leaf dropping in ornamental plants by removing ethylene from greenhouses using fans and ventilation.

Nontraditional Hormones

Recent research has discovered a number of compounds that also influence plant development. Their roles are less understood than the effects of the major hormones described so far.

Jasmonates play a major role in defense responses to herbivory. Their levels increase when a plant is wounded by a predator, resulting in an increase in toxic secondary metabolites. They contribute to the production of volatile compounds that attract natural enemies of predators. For example, chewing of tomato plants by caterpillars leads to an increase in jasmonic acid levels, which in turn triggers the release of volatile compounds that attract predators of the pest.

Oligosaccharins also play a role in plant defense against bacterial and fungal infections. They act locally at the site of injury, and can also be transported to other tissues. **Strigolactones** promote seed germination in some species and inhibit lateral apical development in the absence of auxins. Strigolactones also play a role in the establishment of mycorrhizae, a mutualistic association of plant roots and fungi. Brassinosteroids are important to many developmental and physiological processes. Signals between these compounds and other hormones, notably auxin and GAs, amplifies their physiological effect. Apical dominance, seed germination, gravitropism, and resistance to freezing are all positively influenced by hormones. Root growth and fruit dropping are inhibited by steroids.

Plant Responses to Wind and Touch

The shoot of a pea plant winds around a trellis, while a tree grows on an angle in response to strong prevailing winds. These are examples of how plants respond to touch or wind.

The movement of a plant subjected to constant directional pressure is called **thigmotropism**, from the Greek words *thigma* meaning "touch," and *tropism* implying "direction." Tendrils are one example of this. The meristematic region of tendrils is very touch sensitive; light touch will evoke a quick coiling response. Cells in contact with a support surface

contract, whereas cells on the opposite side of the support expand ([link]). Application of jasmonic acid is sufficient to trigger tendril coiling without a mechanical stimulus.

A **thigmonastic** response is a touch response independent of the direction of stimulus [link]. In the Venus flytrap, two modified leaves are joined at a hinge and lined with thin fork-like tines along the outer edges. Tiny hairs are located inside the trap. When an insect brushes against these trigger hairs, touching two or more of them in succession, the leaves close quickly, trapping the prey. Glands on the leaf surface secrete enzymes that slowly digest the insect. The released nutrients are absorbed by the leaves, which reopen for the next meal.

Thigmomorphogenesis is a slow developmental change in the shape of a plant subjected to continuous mechanical stress. When trees bend in the wind, for example, growth is usually stunted and the trunk thickens. Strengthening tissue, especially xylem, is produced to add stiffness to resist the wind's force. Researchers hypothesize that mechanical strain induces growth and differentiation to strengthen the tissues. Ethylene and jasmonate are likely involved in thigmomorphogenesis.

Note:
Link to Learning

Use the menu at the left to navigate to three short movies: a Venus fly trap capturing prey, the progressive closing of sensitive plant leaflets, and the twining of tendrils.

Defense Responses against Herbivores and Pathogens

Plants face two types of enemies: herbivores and pathogens. Herbivores both large and small use plants as food, and actively chew them. Pathogens are agents of disease. These infectious microorganisms, such as fungi, bacteria, and nematodes, live off of the plant and damage its tissues. Plants have developed a variety of strategies to discourage or kill attackers.

The first line of defense in plants is an intact and impenetrable barrier. Bark and the waxy cuticle can protect against predators. Other adaptations against herbivory include thorns, which are modified branches, and spines, which are modified leaves. They discourage animals by causing physical damage and inducing rashes and allergic reactions. A plant's exterior protection can be compromised by mechanical damage, which may provide an entry point for pathogens. If the first line of defense is breached, the plant must resort to a different set of defense mechanisms, such as toxins and enzymes.

Secondary metabolites are compounds that are not directly derived from photosynthesis and are not necessary for respiration or plant growth and development. Many metabolites are toxic, and can even be lethal to animals that ingest them. Some metabolites are alkaloids, which discourage predators with noxious odors (such as the volatile oils of mint and sage) or repellent tastes (like the bitterness of quinine). Other alkaloids affect herbivores by causing either excessive stimulation (caffeine is one example) or the lethargy associated with opioids. Some compounds become toxic after ingestion; for instance, glycol cyanide in the cassava root releases cyanide only upon ingestion by the herbivore.

Mechanical wounding and predator attacks activate defense and protection mechanisms both in the damaged tissue and at sites farther from the injury location. Some defense reactions occur within minutes: others over several hours. The infected and surrounding cells may die, thereby stopping the spread of infection.

Long-distance signaling elicits a systemic response aimed at deterring the predator. As tissue is damaged, jasmonates may promote the synthesis of compounds that are toxic to predators. Jasmonates also elicit the synthesis

of volatile compounds that attract parasitoids, which are insects that spend their developing stages in or on another insect, and eventually kill their host. The plant may activate abscission of injured tissue if it is damaged beyond repair.

Section Summary

Plants respond to light by changes in morphology and activity. Irradiation by red light converts the photoreceptor phytochrome to its far-red light-absorbing form—Pfr. This form controls germination and flowering in response to length of day, as well as triggers photosynthesis in dormant plants or those that just emerged from the soil. Blue-light receptors, cryptochromes, and phototropins are responsible for phototropism. Amyloplasts, which contain heavy starch granules, sense gravity. Shoots exhibit negative gravitropism, whereas roots exhibit positive gravitropism. Plant hormones—naturally occurring compounds synthesized in small amounts—can act both in the cells that produce them and in distant tissues and organs. Auxins are responsible for apical dominance, root growth, directional growth toward light, and many other growth responses. Cytokinins stimulate cell division and counter apical dominance in shoots. Gibberellins inhibit dormancy of seeds and promote stem growth. Abscisic acid induces dormancy in seeds and buds, and protects plants from excessive water loss by promoting stomatal closure. Ethylene gas speeds up fruit ripening and dropping of leaves. Plants respond to touch by rapid movements (thigmotropy and thigmonasty) and slow differential growth (thigmomorphogenesis). Plants have evolved defense mechanisms against predators and pathogens. Physical barriers like bark and spines protect tender tissues. Plants also have chemical defenses, including toxic secondary metabolites and hormones, which elicit additional defense mechanisms.

Review Questions

Exercise:

Problem:

The main photoreceptor that triggers phototropism is a _____.

    a. phytochrome
    b. cryptochrome
    c. phototropin
    d. carotenoid

Solution:

C

Exercise:

Problem: Phytochrome is a plant pigment protein that:

    a. mediates plant infection
    b. promotes plant growth
    c. mediates morphological changes in response to red and far-red light
    d. inhibits plant growth

Solution:

C

Exercise:

Problem:

A mutant plant has roots that grow in all directions. Which of the following organelles would you expect to be missing in the cell?

    a. mitochondria
    b. amyloplast
    c. chloroplast

d. nucleus

Solution:

B

Exercise:

Problem:

After buying green bananas or unripe avocadoes, they can be kept in a brown bag to ripen. The hormone released by the fruit and trapped in the bag is probably:

   a. abscisic acid
   b. cytokinin
   c. ethylene
   d. gibberellic acid

Solution:

C

Exercise:

Problem:

A decrease in the level of which hormone releases seeds from dormancy?

   a. abscisic acid
   b. cytokinin
   c. ethylene
   d. gibberellic acid

Solution:

A

Exercise:

Problem:

A seedling germinating under a stone grows at an angle away from the stone and upward. This response to touch is called _____.

    a. gravitropism
    b. thigmonasty
    c. thigmotropism
    d. skototropism

Solution:

C

Free Response

Exercise:

Problem:

Owners and managers of plant nurseries have to plan lighting schedules for a long-day plant that will flower in February. What lighting periods will be most effective? What color of light should be chosen?

Solution:

A long-day plant needs a higher proportion of the Pfr form to Pr form of phytochrome. The plant requires long periods of illumination with light enriched in the red range of the spectrum.

Exercise:

Problem:

What are the major benefits of gravitropism for a germinating seedling?

Solution:

Gravitropism will allow roots to dig deep into the soil to find water and minerals, whereas the seedling will grow towards light to enable photosynthesis.

Exercise:

Problem:

Fruit and vegetable storage facilities are usually refrigerated and well ventilated. Why are these conditions advantageous?

Solution:

Refrigeration slows chemical reactions, including fruit maturation. Ventilation removes the ethylene gas that speeds up fruit ripening.

Exercise:

Problem:

Stomata close in response to bacterial infection. Why is this response a mechanism of defense for the plant? Which hormone is most likely to mediate this response?

Solution:

To prevent further entry of pathogens, stomata close, even if they restrict entry of CO_2. Some pathogens secrete virulence factors that inhibit the closing of stomata. Abscisic acid is the stress hormone responsible for inducing closing of stomata.

Glossary

abscisic acid (ABA)
    plant hormone that induces dormancy in seeds and other organs

abscission
    physiological process that leads to the fall of a plant organ (such as
    leaf or petal drop)

auxin
    plant hormone that influences cell elongation (in phototropism),
    gravitropism, apical dominance and root growth

chromophore
    molecule that absorbs light

cryptochrome
    protein that absorbs light in the blue and ultraviolet regions of the light
    spectrum

cytokinin
    plant hormone that promotes cell division

ethylene
    volatile plant hormone that is associated with fruit ripening, flower
    wilting, and leaf fall

gibberellin (GA)
    plant hormone that stimulates shoot elongation, seed germination, and
    the maturation and dropping of fruit and flowers

jasmonates
    small family of compounds derived from the fatty acid linoleic acid

negative gravitropism
    growth away from Earth's gravity

oligosaccharin
    hormone important in plant defenses against bacterial and fungal
    infections

photomorphogenesis
    growth and development of plants in response to light

photoperiodism
    occurrence of plant processes, such as germination and flowering,
    according to the time of year

phototropin
    blue-light receptor that promotes phototropism, stomatal opening and
    closing, and other responses that promote photosynthesis

phototropism
    directional bending of a plant toward a light source

phytochrome
    plant pigment protein that exists in two reversible forms (Pr and Pfr)
    and mediates morphologic changes in response to red light

positive gravitropism
    growth toward Earth's gravitational center

statolith
    (also, **amyloplast**) plant organelle that contains heavy starch granules

strigolactone
    hormone that promotes seed germination in some species and inhibits
    lateral apical development in the absence of auxins

thigmomorphogenesis
    developmental response to touch

thigmonastic
    directional growth of a plant independent of the direction in which
    contact is applied

thigmotropism
    directional growth of a plant in response to constant contact

Introduction
class="introduction"

Plants that reproduce sexually often achieve fertilization with the help of pollinators such as (a) bees, (b) birds, and (c) butterflies. (credit a: modification of work by John Severns; credit b: modification of work by Charles J. Sharp; credit c: modification of work by "Galawebdesign"/Flickr)
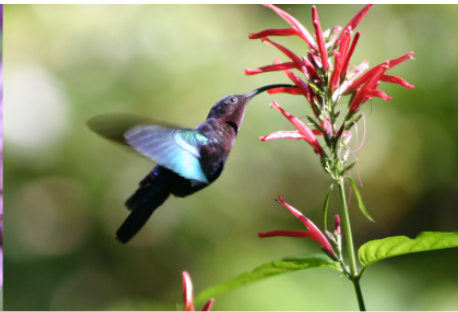
(a)   (b)   (c)

Plants have evolved different reproductive strategies for the continuation of their species. Some plants reproduce sexually, and others asexually, in contrast to animal species, which rely almost exclusively on sexual reproduction. Plant sexual reproduction usually depends on pollinating agents, while asexual reproduction is independent of these agents. Flowers are often the showiest or most strongly scented part of plants. With their bright colors, fragrances, and interesting shapes and sizes, flowers attract

insects, birds, and animals to serve their pollination needs. Other plants pollinate via wind or water; still others self-pollinate.

Reproductive Development and Structure
By the end of this section, you will be able to:

- Describe the two stages of a plant's lifecycle
- Compare and contrast male and female gametophytes and explain how they form in angiosperms
- Describe the reproductive structures of a plant
- Describe the components of a complete flower
- Describe the development of microsporangium and megasporangium in gymnosperms

Sexual reproduction takes place with slight variations in different groups of plants. Plants have two distinct stages in their lifecycle: the gametophyte stage and the sporophyte stage. The haploid **gametophyte** produces the male and female gametes by mitosis in distinct multicellular structures. Fusion of the male and females gametes forms the diploid zygote, which develops into the **sporophyte**. After reaching maturity, the diploid sporophyte produces spores by meiosis, which in turn divide by mitosis to produce the haploid gametophyte. The new gametophyte produces gametes, and the cycle continues. This is the alternation of generations, and is typical of plant reproduction ([link]).
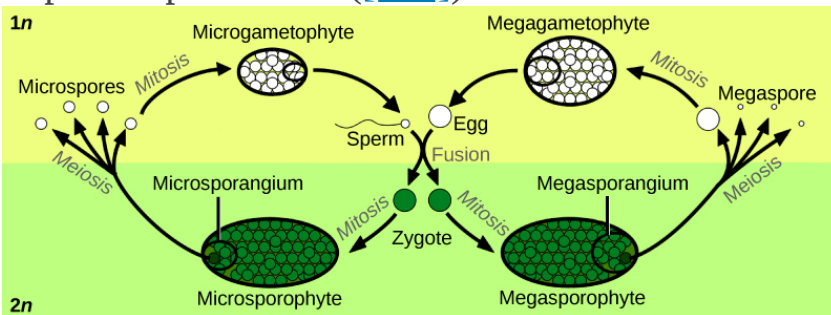
The alternation of generations in angiosperms
is depicted in this diagram. (credit:
modification of work by Peter Coxhead)

The life cycle of higher plants is dominated by the sporophyte stage, with the gametophyte borne on the sporophyte. In ferns, the gametophyte is free-

living and very distinct in structure from the diploid sporophyte. In bryophytes, such as mosses, the haploid gametophyte is more developed than the sporophyte.

During the vegetative phase of growth, plants increase in size and produce a shoot system and a root system. As they enter the reproductive phase, some of the branches start to bear flowers. Many flowers are borne singly, whereas some are borne in clusters. The flower is borne on a stalk known as a receptacle. Flower shape, color, and size are unique to each species, and are often used by taxonomists to classify plants.

Sexual Reproduction in Angiosperms

The lifecycle of angiosperms follows the alternation of generations explained previously. The haploid gametophyte alternates with the diploid sporophyte during the sexual reproduction process of angiosperms. Flowers contain the plant's reproductive structures.

Flower Structure

A typical flower has four main parts—or whorls—known as the calyx, corolla, androecium, and gynoecium ([link]). The outermost whorl of the flower has green, leafy structures known as sepals. The sepals, collectively called the calyx, help to protect the unopened bud. The second whorl is comprised of petals—usually, brightly colored—collectively called the corolla. The number of sepals and petals varies depending on whether the plant is a monocot or dicot. In monocots, petals usually number three or multiples of three; in dicots, the number of petals is four or five, or multiples of four and five. Together, the calyx and corolla are known as the **perianth**. The third whorl contains the male reproductive structures and is known as the androecium. The **androecium** has stamens with anthers that contain the microsporangia. The innermost group of structures in the flower is the **gynoecium**, or the female reproductive component(s). The carpel is the individual unit of the gynoecium and has a stigma, style, and ovary. A flower may have one or multiple carpels.
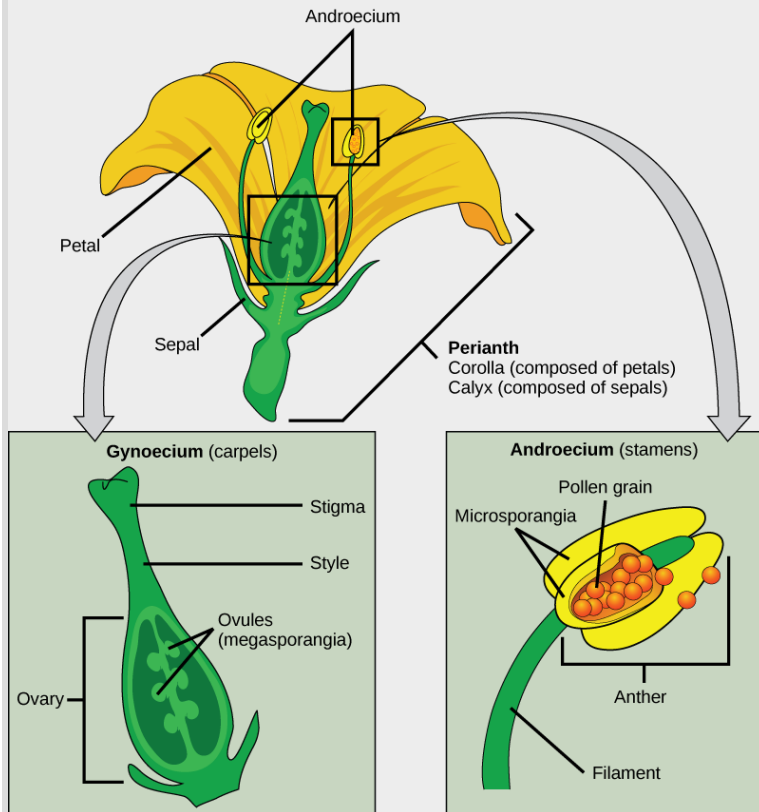
The four main parts of the flower are the calyx, corolla, androecium, and gynoecium. The androecium is the sum of all the male reproductive organs, and the gynoecium is the sum of the female reproductive organs. (credit: modification of work by Mariana Ruiz Villareal)

If the anther is missing, what type of reproductive structure will the flower be unable to produce? What term is used to describe an incomplete flower lacking the androecium? What term describes an incomplete flower lacking a gynoecium?

If all four whorls (the calyx, corolla, androecium, and gynoecium) are present, the flower is described as complete. If any of the four parts is missing, the flower is known as incomplete. Flowers that contain both an androecium and a gynoecium are called perfect, androgynous or hermaphrodites. There are two types of incomplete flowers: staminate flowers contain only an androecium, and carpellate flowers have only a gynoecium ([link]).

The corn plant has both staminate (male) and carpellate (female) flowers. Staminate flowers, which are clustered in the tassel at the tip of the stem, produce pollen grains. Carpellate flower are clustered in

the immature ears. Each strand of silk is a stigma. The corn kernels are seeds that develop on the ear after fertilization. Also shown is the lower stem and root.

If both male and female flowers are borne on the same plant, the species is called monoecious (meaning "one home"): examples are corn and pea. Species with male and female flowers borne on separate plants are termed dioecious, or "two homes," examples of which are *C. papaya* and *Cannabis*. The ovary, which may contain one or multiple ovules, may be placed above other flower parts, which is referred to as superior; or, it may be placed below the other flower parts, referred to as inferior ([link]).
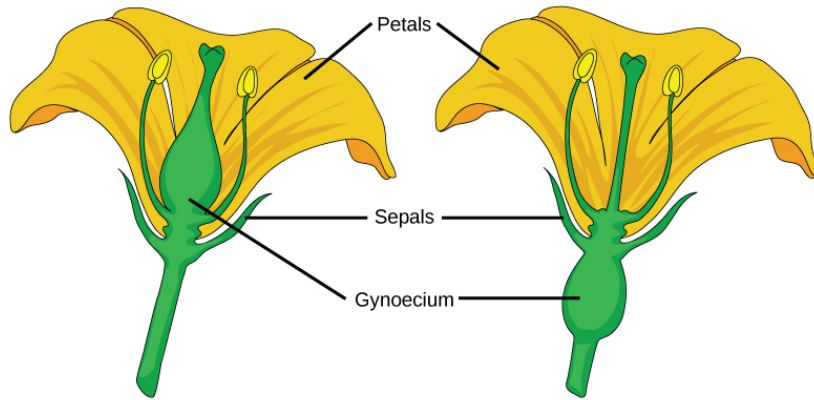
The (a) lily is a superior flower, which has the ovary above the other flower parts. (b) Fuchsia is an inferior flower, which has the ovary beneath other flower parts. (credit a photo: modification of work by Benjamin Zwittnig; credit b photo: modification of work by "Koshy Koshy"/Flickr)

Male Gametophyte (The Pollen Grain)

The male gametophyte develops and reaches maturity in an immature anther. In a plant's male reproductive organs, development of pollen takes

place in a structure known as the **microsporangium** ([link]). The microsporangia, which are usually bi-lobed, are pollen sacs in which the microspores develop into pollen grains. These are found in the anther, which is at the end of the stamen—the long filament that supports the anther.
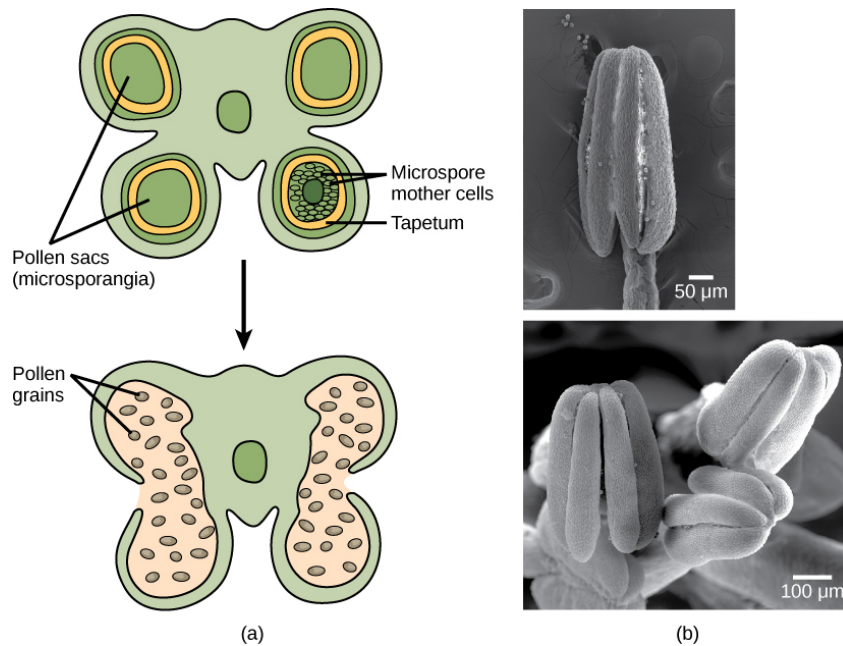
Shown is (a) a cross section of an anther at two developmental stages. The immature anther (top) contains four microsporangia, or pollen sacs. Each microsporangium contains hundreds of microspore mother cells that will each give rise to four pollen grains. The tapetum supports the development and maturation of the pollen grains. Upon maturation of the pollen (bottom), the pollen sac walls split open and the pollen grains (male gametophytes) are released. (b) In these scanning electron micrographs, pollen sacs are ready to burst, releasing their grains. (credit b: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Within the microsporangium, the microspore mother cell divides by meiosis to give rise to four microspores, each of which will ultimately form a pollen grain ([link]). An inner layer of cells, known as the tapetum, provides nutrition to the developing microspores and contributes key components to the pollen wall. Mature pollen grains contain two cells: a generative cell and a pollen tube cell. The generative cell is contained within the larger pollen tube cell. Upon germination, the tube cell forms the pollen tube through which the generative cell migrates to enter the ovary. During its transit inside the pollen tube, the generative cell divides to form two male gametes (sperm cells). Upon maturity, the microsporangia burst, releasing the pollen grains from the anther.
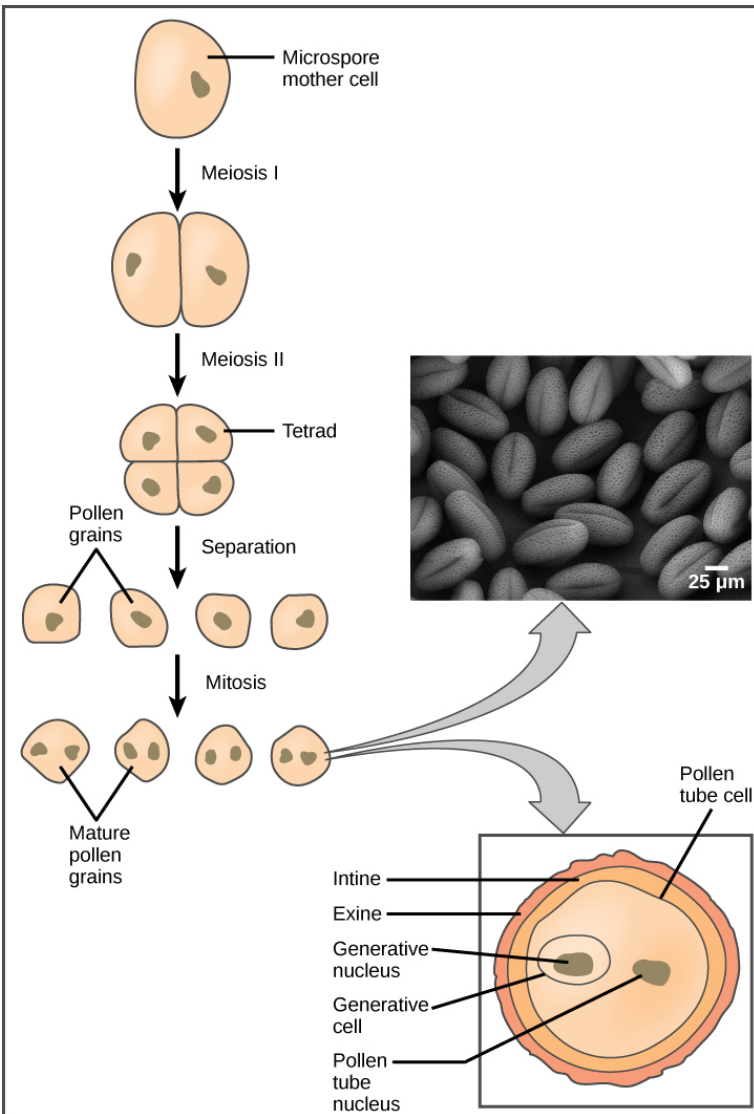
Pollen develops from the microspore mother cells. The mature pollen grain is composed of two cells: the pollen tube cell and the generative cell, which is inside the tube cell. The pollen grain has two coverings: an inner layer (intine) and an outer layer (exine). The inset scanning electron micrograph shows *Arabidopsis lyrata* pollen grains. (credit "pollen micrograph": modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Each pollen grain has two coverings: the **exine** (thicker, outer layer) and the **intine** ([link]). The exine contains sporopollenin, a complex waterproofing substance supplied by the tapetal cells. Sporopollenin allows the pollen to survive under unfavorable conditions and to be carried by wind, water, or biological agents without undergoing damage.

Female Gametophyte (The Embryo Sac)

While the details may vary between species, the overall development of the female gametophyte has two distinct phases. First, in the process of **megasporogenesis**, a single cell in the diploid **megasporangium**—an area of tissue in the ovules—undergoes meiosis to produce four megaspores, only one of which survives. During the second phase, **megagametogenesis**, the surviving haploid megaspore undergoes mitosis to produce an eight-nucleate, seven-cell female gametophyte, also known as the megagametophyte or embryo sac. Two of the nuclei—the **polar nuclei**—move to the equator and fuse, forming a single, diploid central cell. This central cell later fuses with a sperm to form the triploid endosperm. Three nuclei position themselves on the end of the embryo sac opposite the micropyle and develop into the **antipodal** cells, which later degenerate. The nucleus closest to the micropyle becomes the female gamete, or egg cell, and the two adjacent nuclei develop into **synergid** cells ([link]). The synergids help guide the pollen tube for successful fertilization, after which they disintegrate. Once fertilization is complete, the resulting diploid zygote develops into the embryo, and the fertilized ovule forms the other tissues of the seed.

A double-layered integument protects the megasporangium and, later, the embryo sac. The integument will develop into the seed coat after fertilization and protect the entire seed. The ovule wall will become part of the fruit. The integuments, while protecting the megasporangium, do not enclose it completely, but leave an opening called the **micropyle**. The

micropyle allows the pollen tube to enter the female gametophyte for fertilization.

Embryo Sac

Chalazal end

Antipodals

Polar nuclei

Synergids

Egg cell

Central cell

Micropylar end
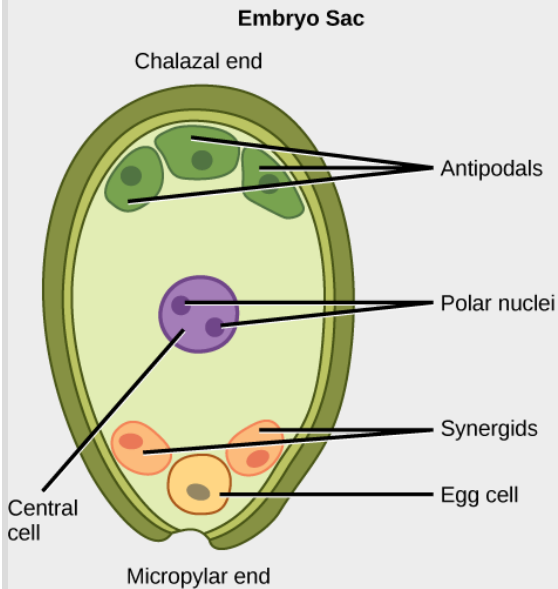
As shown in this diagram of the embryo sac in angiosperms, the ovule is covered by integuments and has an opening called a micropyle. Inside the embryo sac are three antipodal cells, two synergids, a central cell, and the egg cell.

An embryo sac is missing the synergids. What specific impact would you expect this to have on fertilization?

a. The pollen tube will be unable to form.
b. The pollen tube will form but will not be guided toward the egg.

c. Fertilization will not occur because the synergid is the egg.
d. Fertilization will occur but the embryo will not be able to grow.

Sexual Reproduction in Gymnosperms

As with angiosperms, the lifecycle of a gymnosperm is also characterized by alternation of generations. In conifers such as pines, the green leafy part of the plant is the sporophyte, and the cones contain the male and female gametophytes ([link]). The female cones are larger than the male cones and are positioned towards the top of the tree; the small, male cones are located in the lower region of the tree. Because the pollen is shed and blown by the wind, this arrangement makes it difficult for a gymnosperm to self-pollinate.
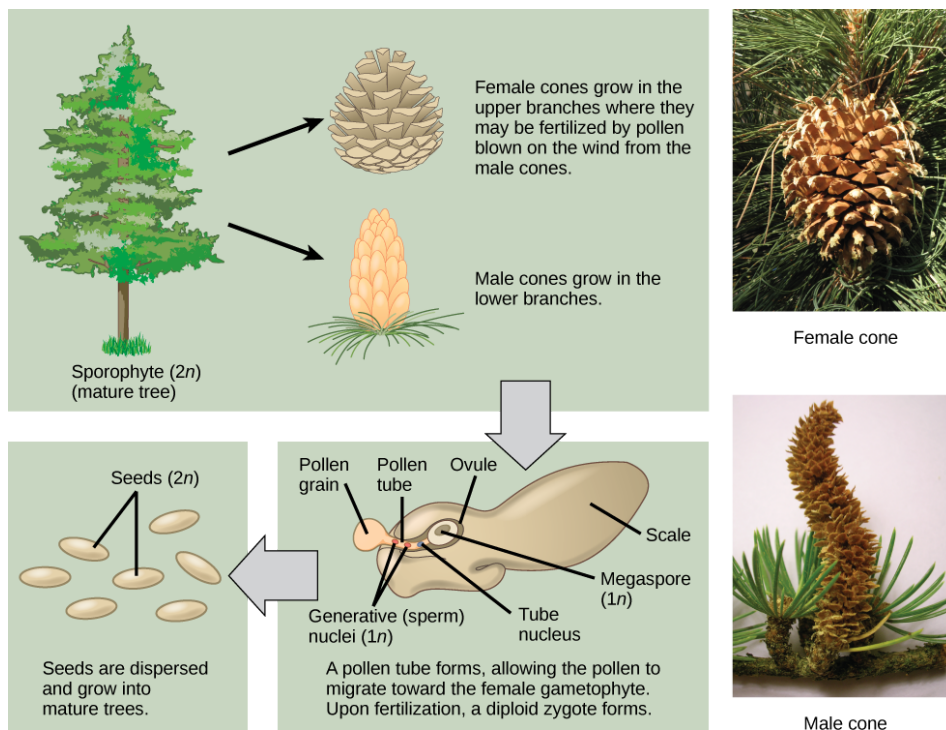
Female cones grow in the upper branches where they may be fertilized by pollen blown on the wind from the male cones.

Male cones grow in the lower branches.

Sporophyte (2n)
(mature tree)

Female cone

Seeds (2n)

Pollen grain   Pollen tube   Ovule

Scale

Megaspore (1n)

Generative (sperm) nuclei (1n)   Tube nucleus

Seeds are dispersed and grow into mature trees.

A pollen tube forms, allowing the pollen to migrate toward the female gametophyte. Upon fertilization, a diploid zygote forms.

Male cone

This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where

it fertilizes female cones. Examples are shown of female and male cones. (credit "female": modification of work by "Geographer"/Wikimedia Commons; credit "male": modification of work by Roger Griffith)

Male Gametophyte

A male cone has a central axis on which bracts, a type of modified leaf, are attached. The bracts are known as **microsporophylls** ([link]) and are the sites where microspores will develop. The microspores develop inside the microsporangium. Within the microsporangium, cells known as microsporocytes divide by meiosis to produce four haploid microspores. Further mitosis of the microspore produces two nuclei: the generative nucleus, and the tube nucleus. Upon maturity, the male gametophyte (pollen) is released from the male cones and is carried by the wind to land on the female cone.

Note:
Link to Learning

Watch this video to see a cedar releasing its pollen in the wind.
https://www.openstaxcollege.org/l/pollen_release

Female Gametophyte

The female cone also has a central axis on which bracts known as **megasporophylls** ([link]) are present. In the female cone, megaspore mother cells are present in the megasporangium. The megaspore mother cell divides by meiosis to produce four haploid megaspores. One of the megaspores divides to form the multicellular female gametophyte, while the others divide to form the rest of the structure. The female gametophyte is contained within a structure called the archegonium.
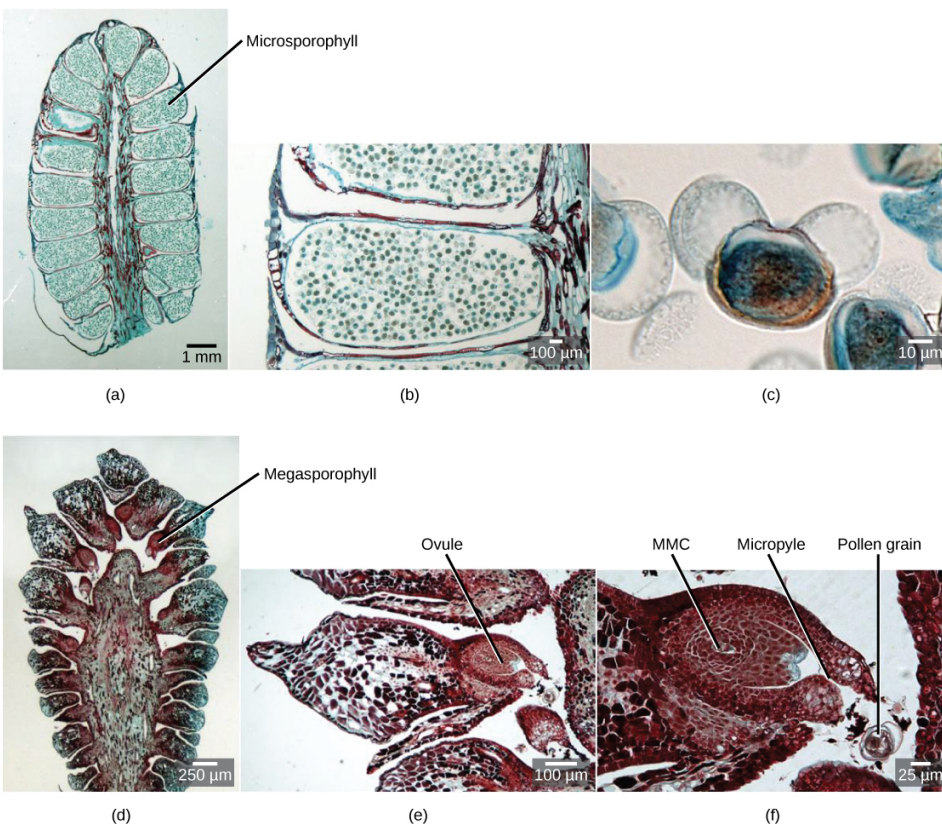
These series of micrographs shows male and female gymnosperm gametophytes. (a) This male cone, shown in cross section, has approximately 20 microsporophylls, each of which produces hundreds of male gametophytes (pollen grains). (b) Pollen grains are visible in this single microsporophyll. (c) This micrograph shows an individual pollen grain. (d)

This cross section of a female cone shows portions of about 15 megasporophylls. (e) The ovule can be seen in this single megasporophyll. (f) Within this single ovule are the megaspore mother cell (MMC), micropyle, and a pollen grain. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Reproductive Process

Upon landing on the female cone, the tube cell of the pollen forms the pollen tube, through which the generative cell migrates towards the female gametophyte through the micropyle. It takes approximately one year for the pollen tube to grow and migrate towards the female gametophyte. The male gametophyte containing the generative cell splits into two sperm nuclei, one of which fuses with the egg, while the other degenerates. After fertilization of the egg, the diploid zygote is formed, which divides by mitosis to form the embryo. The scales of the cones are closed during development of the seed. The seed is covered by a seed coat, which is derived from the female sporophyte. Seed development takes another one to two years. Once the seed is ready to be dispersed, the bracts of the female cones open to allow the dispersal of seed; no fruit formation takes place because gymnosperm seeds have no covering.

Angiosperms versus Gymnosperms

Gymnosperm reproduction differs from that of angiosperms in several ways ([link]). In angiosperms, the female gametophyte exists in an enclosed structure—the ovule—which is within the ovary; in gymnosperms, the female gametophyte is present on exposed bracts of the female cone. Double fertilization is a key event in the lifecycle of angiosperms, but is completely absent in gymnosperms. The male and female gametophyte structures are present on separate male and female cones in gymnosperms,

whereas in angiosperms, they are a part of the flower. Lastly, wind plays an important role in pollination in gymnosperms because pollen is blown by the wind to land on the female cones. Although many angiosperms are also wind-pollinated, animal pollination is more common.

(a)   (b)

(a) Angiosperms are flowering plants, and include grasses, herbs, shrubs and most deciduous trees, while (b) gymnosperms are conifers. Both produce seeds but have different reproductive strategies. (credit a: modification of work by Wendy Cutler; credit b: modification of work by Lews Castle UHI)

Note:
Link to Learning

Section Summary

The flower contains the reproductive structures of a plant. All complete flowers contain four whorls: the calyx, corolla, androecium, and gynoecium. The stamens are made up of anthers, in which pollen grains are produced, and a supportive strand called the filament. The pollen contains two cells— a generative cell and a tube cell—and is covered by two layers called the intine and the exine. The carpels, which are the female reproductive structures, consist of the stigma, style, and ovary. The female gametophyte is formed from mitotic divisions of the megaspore, forming an eight-nuclei ovule sac. This is covered by a layer known as the integument. The integument contains an opening called the micropyle, through which the pollen tube enters the embryo sac.

The diploid sporophyte of angiosperms and gymnosperms is the conspicuous and long-lived stage of the life cycle. The sporophytes differentiate specialized reproductive structures called sporangia, which are dedicated to the production of spores. The microsporangium contains microspore mother cells, which divide by meiosis to produce haploid microspores. The microspores develop into male gametophytes that are released as pollen. The megasporangium contains megaspore mother cells, which divide by meiosis to produce haploid megaspores. A megaspore develops into a female gametophyte containing a haploid egg. A new diploid sporophyte is formed when a male gamete from a pollen grain enters the ovule sac and fertilizes this egg.

Art Connections

Exercise:

Problem:

[link] If the anther is missing, what type of reproductive structure will the flower be unable to produce? What term is used to describe a flower that is normally lacking the androecium? What term describes a flower lacking a gynoecium?

Solution:

[link] Pollen (or sperm); carpellate; staminate.

Exercise:

Problem:

[link] An embryo sac is missing the synergids. What specific impact would you expect this to have on fertilization?

   a. The pollen tube will be unable to form.
   b. The pollen tube will form but will not be guided toward the egg.
   c. Fertilization will not occur because the synergid is the egg.
   d. Fertilization will occur but the embryo will not be able to grow.

Solution:

[link] B: The pollen tube will form but will not be guided toward the egg.

Review Questions

Exercise:

Problem:

In a plant's male reproductive organs, development of pollen takes place in a structure known as the _____.

    a. stamen
    b. microsporangium
    c. anther
    d. tapetum

Solution:

  B

Exercise:

Problem:

The stamen consists of a long stalk called the filament that supports the _____.

    a. stigma
    b. sepal
    c. style
    d. anther

Solution:

  D

Exercise:

Problem: The _____ are collectively called the calyx.

    a. sepals
    b. petals
    c. tepals

d. stamens

Solution:

A

Exercise:

Problem: The pollen lands on which part of the flower?

    a. stigma
    b. style
    c. ovule
    d. integument

Solution:

A

Free Response

Exercise:

Problem: Describe the reproductive organs inside a flower.

Solution:

Inside the flower are the reproductive organs of the plant. The stamen is the male reproductive organ. Pollen is produced in the stamen. The carpel is the female reproductive organ. The ovary is the swollen base of the carpel where ovules are found. Not all flowers have every one of the four parts.

Exercise:

Problem:

Describe the two-stage lifecycle of plants: the gametophyte stage and the sporophyte stage.

Solution:

Plants have two distinct phases in their lifecycle: the gametophyte stage and the sporophyte stage. In the gametophyte stage, when reproductive cells undergo meiosis and produce haploid cells called spores, the gametophyte stage begins. Spores divide by cell division to form plant structures of an entirely new plant. The cells in these structures or plants are haploid. Some of these cells undergo cell division and form sex cells. Fertilization, the joining of haploid sex cells, begins the sporophyte stage. Cells formed in this stage have the diploid number of chromosomes. Meiosis in some of these cells forms spores, and the cycle begins again: a process known as alternation of generations.

Exercise:

Problem: Describe the four main parts, or whorls, of a flower.

Solution:

A typical flower has four main parts, or whorls: the calyx, corolla, androecium, and gynoecium. The outermost whorl of the flower has green, leafy structures known as sepals, which are collectively called the calyx. It helps to protect the unopened bud. The second whorl is made up of brightly colored petals that are known collectively as the corolla. The third whorl is the male reproductive structure known as the androecium. The androecium has stamens, which have anthers on a stalk or filament. Pollen grains are borne on the anthers. The gynoecium is the female reproductive structure. The carpel is the individual structure of the gynoecium and has a stigma, the stalk or style, and the ovary.

Exercise:

Problem:

Discuss the differences between a complete flower and an incomplete flower.

Solution:

If all four whorls of a flower are present, it is a complete flower. If any of the four parts is missing, it is known as incomplete. Flowers that contain both an androecium and gynoecium are called androgynous or hermaphrodites. Those that contain only an androecium are known as staminate flowers, and those that have only carpels are known as carpellate. If both male and female flowers are borne on the same plant, it is called monoecious, while plants with male and female flowers on separate plants are termed dioecious.

Glossary

androecium
    sum of all the stamens in a flower

antipodals
    the three cells away from the micropyle

exine
    outermost covering of pollen

gametophyte
    multicellular stage of the plant that gives rise to haploid gametes or spores

gynoecium
    the sum of all the carpels in a flower

intine
    inner lining of the pollen

megagametogenesis
second phase of female gametophyte development, during which the surviving haploid megaspore undergoes mitosis to produce an eight-nucleate, seven-cell female gametophyte, also known as the megagametophyte or embryo sac.

megasporangium
tissue found in the ovary that gives rise to the female gamete or egg

megasporogenesis
first phase of female gametophyte development, during which a single cell in the diploid megasporangium undergoes meiosis to produce four megaspores, only one of which survives

megasporophyll
bract (a type of modified leaf) on the central axis of a female gametophyte

micropyle
opening on the ovule sac through which the pollen tube can gain entry

microsporangium
tissue that gives rise to the microspores or the pollen grain

microsporophyll
central axis of a male cone on which bracts (a type of modified leaf) are attached

perianth
(also, petal or sepal) part of the flower consisting of the calyx and/or corolla; forms the outer envelope of the flower

polar nuclei
found in the ovule sac; fusion with one sperm cell forms the endosperm

sporophyte

multicellular diploid stage in plants that is formed after the fusion of male and female gametes

synergid
type of cell found in the ovule sac that secretes chemicals to guide the pollen tube towards the egg

Pollination and Fertilization
By the end of this section, you will be able to:

- Describe what must occur for plant fertilization
- Explain cross-pollination and the ways in which it takes place
- Describe the process that leads to the development of a seed
- Define double fertilization

In angiosperms, **pollination** is defined as the placement or transfer of pollen from the anther to the stigma of the same flower or another flower. In gymnosperms, pollination involves pollen transfer from the male cone to the female cone. Upon transfer, the pollen germinates to form the pollen tube and the sperm for fertilizing the egg. Pollination has been well studied since the time of Gregor Mendel. Mendel successfully carried out self- as well as cross-pollination in garden peas while studying how characteristics were passed on from one generation to the next. Today's crops are a result of plant breeding, which employs artificial selection to produce the present-day cultivars. A case in point is today's corn, which is a result of years of breeding that started with its ancestor, teosinte. The teosinte that the ancient Mayans originally began cultivating had tiny seeds—vastly different from today's relatively giant ears of corn. Interestingly, though these two plants appear to be entirely different, the genetic difference between them is miniscule.

Pollination takes two forms: self-pollination and cross-pollination. **Self-pollination** occurs when the pollen from the anther is deposited on the stigma of the same flower, or another flower on the same plant. **Cross-pollination** is the transfer of pollen from the anther of one flower to the stigma of another flower on a different individual of the same species. Self-pollination occurs in flowers where the stamen and carpel mature at the same time, and are positioned so that the pollen can land on the flower's stigma. This method of pollination does not require an investment from the plant to provide nectar and pollen as food for pollinators.

Note:
Link to Learning

Explore this interactive website to review self-pollination and cross-pollination.

Living species are designed to ensure survival of their progeny; those that fail become extinct. Genetic diversity is therefore required so that in changing environmental or stress conditions, some of the progeny can survive. Self-pollination leads to the production of plants with less genetic diversity, since genetic material from the same plant is used to form gametes, and eventually, the zygote. In contrast, cross-pollination—or out-crossing—leads to greater genetic diversity because the microgametophyte and megagametophyte are derived from different plants.

Because cross-pollination allows for more genetic diversity, plants have developed many ways to avoid self-pollination. In some species, the pollen and the ovary mature at different times. These flowers make self-pollination nearly impossible. By the time pollen matures and has been shed, the stigma of this flower is mature and can only be pollinated by pollen from another flower. Some flowers have developed physical features that prevent self-pollination. The primrose is one such flower. Primroses have evolved two flower types with differences in anther and stigma length: the pin-eyed flower has anthers positioned at the pollen tube's halfway point, and the thrum-eyed flower's stigma is likewise located at the halfway point. Insects easily cross-pollinate while seeking the nectar at the bottom of the pollen tube. This phenomenon is also known as heterostyly. Many plants, such as cucumber, have male and female flowers located on different parts of the plant, thus making self-pollination difficult. In yet other species, the male and female flowers are borne on different plants (dioecious). All of these are barriers to self-pollination; therefore, the plants depend on pollinators to transfer pollen. The majority of pollinators are biotic agents such as insects

(like bees, flies, and butterflies), bats, birds, and other animals. Other plant species are pollinated by abiotic agents, such as wind and water.

Pollination by Insects

Bees are perhaps the most important pollinator of many garden plants and most commercial fruit trees ([link]). The most common species of bees are bumblebees and honeybees. Since bees cannot see the color red, bee-pollinated flowers usually have shades of blue, yellow, or other colors. Bees collect energy-rich pollen or nectar for their survival and energy needs.

They visit flowers that are open during the day, are brightly colored, have a strong aroma or scent, and have a tubular shape, typically with the presence of a nectar guide. A **nectar guide** includes regions on the flower petals that are visible only to bees, and not to humans; it helps to guide bees to the center of the flower, thus making the pollination process more efficient. The pollen sticks to the bees' fuzzy hair, and when the bee visits another flower, some of the pollen is transferred to the second flower. Recently, there have been many reports about the declining population of honeybees. Many flowers will remain unpollinated and not bear seed if honeybees disappear. The impact on commercial fruit growers could be devastating.

Insects, such as bees, are important agents of pollination. (credit: modification of work by Jon Sullivan)

Many flies are attracted to flowers that have a decaying smell or an odor of rotting flesh. These flowers, which produce nectar, usually have dull colors, such as brown or purple. They are found on the corpse flower or voodoo lily (*Amorphophallus*), dragon arum (*Dracunculus*), and carrion flower (*Stapleia*, *Rafflesia*). The nectar provides energy, whereas the pollen

provides protein. Wasps are also important insect pollinators, and pollinate many species of figs.

Butterflies, such as the monarch, pollinate many garden flowers and wildflowers, which usually occur in clusters. These flowers are brightly colored, have a strong fragrance, are open during the day, and have nectar guides to make access to nectar easier. The pollen is picked up and carried on the butterfly's limbs. Moths, on the other hand, pollinate flowers during the late afternoon and night. The flowers pollinated by moths are pale or white and are flat, enabling the moths to land. One well-studied example of a moth-pollinated plant is the yucca plant, which is pollinated by the yucca moth. The shape of the flower and moth have adapted in such a way as to allow successful pollination. The moth deposits pollen on the sticky stigma for fertilization to occur later. The female moth also deposits eggs into the ovary. As the eggs develop into larvae, they obtain food from the flower and developing seeds. Thus, both the insect and flower benefit from each other in this symbiotic relationship. The corn earworm moth and Gaura plant have a similar relationship ([link]).

A corn earworm sips nectar from a night-blooming Gaura plant. (credit: Juan Lopez, USDA ARS)

Pollination by Bats

In the tropics and deserts, bats are often the pollinators of nocturnal flowers such as agave, guava, and morning glory. The flowers are usually large and white or pale-colored; thus, they can be distinguished from the dark surroundings at night. The flowers have a strong, fruity, or musky fragrance and produce large amounts of nectar. They are naturally large and wide-mouthed to accommodate the head of the bat. As the bats seek the nectar, their faces and heads become covered with pollen, which is then transferred to the next flower.

Pollination by Birds

Many species of small birds, such as the hummingbird ([link]) and sun birds, are pollinators for plants such as orchids and other wildflowers. Flowers visited by birds are usually sturdy and are oriented in such a way as to allow the birds to stay near the flower without getting their wings entangled in the nearby flowers. The flower typically has a curved, tubular shape, which allows access for the bird's beak. Brightly colored, odorless flowers that are open during the day are pollinated by birds. As a bird seeks energy-rich nectar, pollen is deposited on the bird's head and neck and is then transferred to the next flower it visits. Botanists have been known to determine the range of extinct plants by collecting and identifying pollen from 200-year-old bird specimens from the same site.

Hummingbirds have adaptations that allow them to reach the nectar of certain tubular flowers. (credit: Lori Branham)

Pollination by Wind

Most species of conifers, and many angiosperms, such as grasses, maples and oaks, are pollinated by wind. Pine cones are brown and unscented, while the flowers of wind-pollinated angiosperm species are usually green, small, may have small or no petals, and produce large amounts of pollen. Unlike the typical insect-pollinated flowers, flowers adapted to pollination by wind do not produce nectar or scent. In wind-pollinated species, the microsporangia hang out of the flower, and, as the wind blows, the lightweight pollen is carried with it ([link]). The flowers usually emerge early in the spring, before the leaves, so that the leaves do not block the movement of the wind. The pollen is deposited on the exposed feathery stigma of the flower ([link]).

A person knocks pollen from a
pine tree.
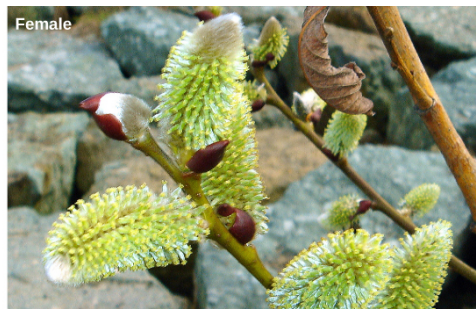
These male (a) and female (b) catkins are from the goat
willow tree (*Salix caprea*). Note how both structures are
light and feathery to better disperse and catch the wind-
blown pollen.

Pollination by Water

Some weeds, such as Australian sea grass and pond weeds, are pollinated by water. The pollen floats on water, and when it comes into contact with the flower, it is deposited inside the flower.

Note:
Evolution Connection
Pollination by Deception
Orchids are highly valued flowers, with many rare varieties ([link]). They grow in a range of specific habitats, mainly in the tropics of Asia, South America, and Central America. At least 25,000 species of orchids have been identified.

Certain orchids use food deception or sexual deception to attract pollinators. Shown here is a bee orchid (*Ophrys apifera*). (credit: David Evans)

Flowers often attract pollinators with food rewards, in the form of nectar. However, some species of orchid are an exception to this standard: they have evolved different ways to attract the desired pollinators. They use a method known as food deception, in which bright colors and perfumes are offered, but no food. *Anacamptis morio*, commonly known as the green-winged orchid, bears bright purple flowers and emits a strong scent. The bumblebee, its main pollinator, is attracted to the flower because of the strong scent—which usually indicates food for a bee—and in the process, picks up the pollen to be transported to another flower.

Other orchids use sexual deception. *Chiloglottis trapeziformis* emits a compound that smells the same as the pheromone emitted by a female wasp to attract male wasps. The male wasp is attracted to the scent, lands on the orchid flower, and in the process, transfers pollen. Some orchids, like the Australian hammer orchid, use scent as well as visual trickery in yet another sexual deception strategy to attract wasps. The flower of this orchid mimics the appearance of a female wasp and emits a pheromone. The male wasp tries to mate with what appears to be a female wasp, and in the process, picks up pollen, which it then transfers to the next counterfeit mate.

Double Fertilization

After pollen is deposited on the stigma, it must germinate and grow through the style to reach the ovule. The microspores, or the pollen, contain two cells: the pollen tube cell and the generative cell. The pollen tube cell grows into a pollen tube through which the generative cell travels. The germination of the pollen tube requires water, oxygen, and certain chemical signals. As it travels through the style to reach the embryo sac, the pollen tube's growth is supported by the tissues of the style. In the meantime, if the generative cell has not already split into two cells, it now divides to form two sperm cells. The pollen tube is guided by the chemicals secreted by the synergids present in the embryo sac, and it enters the ovule sac through the micropyle. Of the two sperm cells, one sperm fertilizes the egg cell, forming a diploid zygote; the other sperm fuses with the two polar nuclei,

forming a triploid cell that develops into the **endosperm**. Together, these two fertilization events in angiosperms are known as **double fertilization** ([link]). After fertilization is complete, no other sperm can enter. The fertilized ovule forms the seed, whereas the tissues of the ovary become the fruit, usually enveloping the seed.
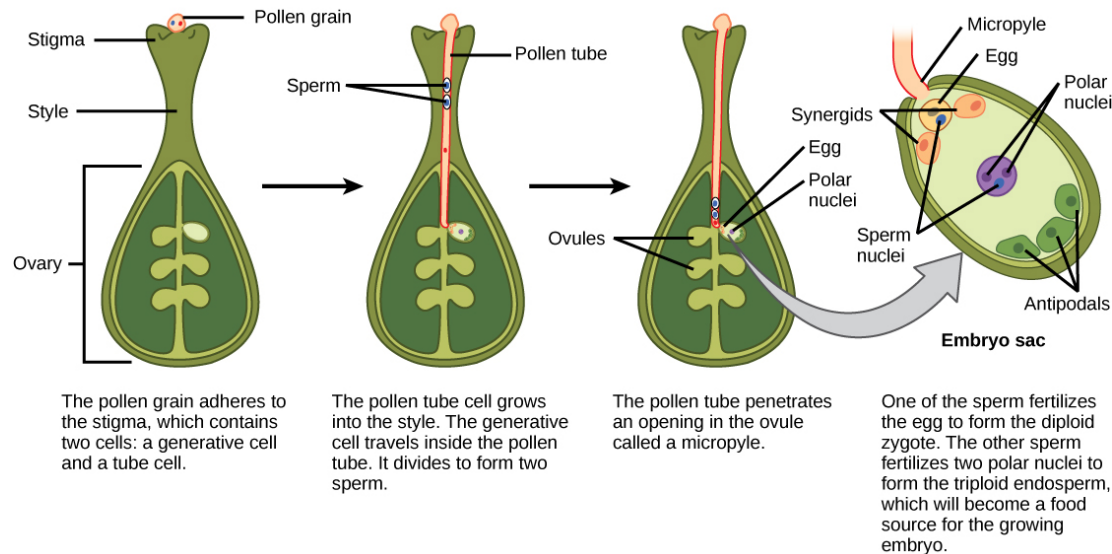
In angiosperms, one sperm fertilizes the egg to form the 2*n* zygote, and the other sperm fertilizes the central cell to form the 3*n* endosperm. This is called a double fertilization.

After fertilization, the zygote divides to form two cells: the upper cell, or terminal cell, and the lower, or basal, cell. The division of the basal cell gives rise to the **suspensor**, which eventually makes connection with the maternal tissue. The suspensor provides a route for nutrition to be transported from the mother plant to the growing embryo. The terminal cell also divides, giving rise to a globular-shaped proembryo ([link]**a**). In dicots (eudicots), the developing embryo has a heart shape, due to the presence of the two rudimentary **cotyledons** ([link]**b**). In non-endospermic dicots, such as *Capsella bursa*, the endosperm develops initially, but is then digested, and the food reserves are moved into the two cotyledons. As the embryo

and cotyledons enlarge, they run out of room inside the developing seed, and are forced to bend ([link]**c**). Ultimately, the embryo and cotyledons fill the seed ([link]**d**), and the seed is ready for dispersal. Embryonic development is suspended after some time, and growth is resumed only when the seed germinates. The developing seedling will rely on the food reserves stored in the cotyledons until the first set of leaves begin photosynthesis.
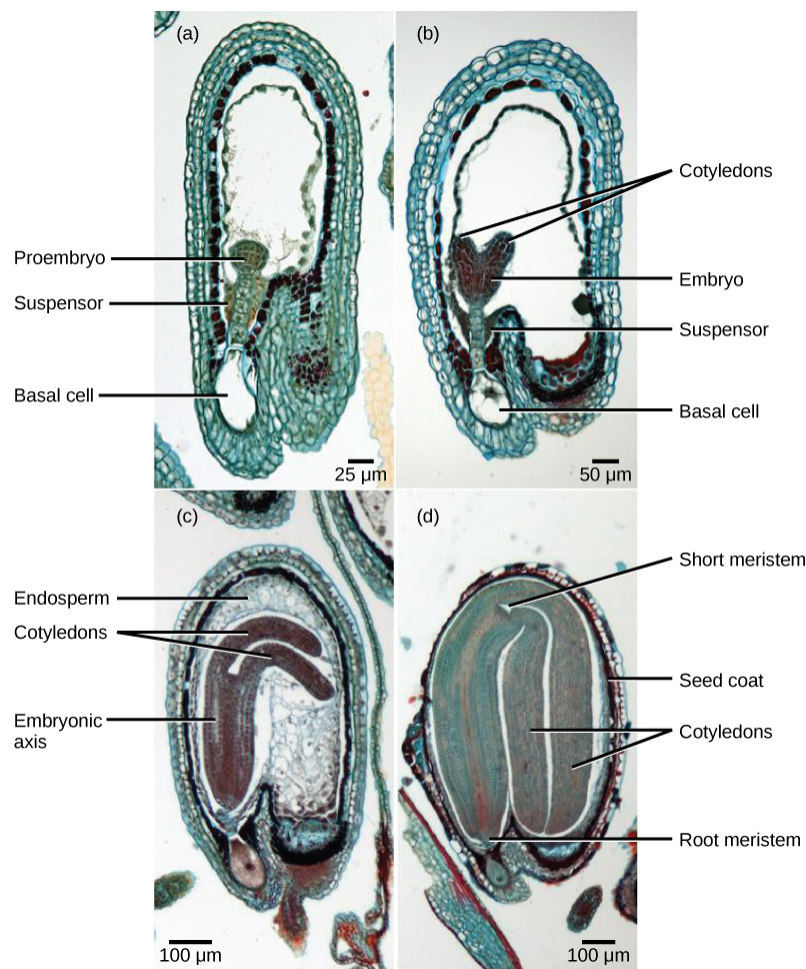
Shown are the stages of embryo development in the ovule of a shepherd's purse (*Capsella bursa*). After fertilization, the zygote divides to form an upper terminal cell and a lower basal cell. (a) In the first

stage of development, the terminal cell divides, forming a globular pro-embryo. The basal cell also divides, giving rise to the suspensor. (b) In the second stage, the developing embryo has a heart shape due to the presence of cotyledons. (c) In the third stage, the growing embryo runs out of room and starts to bend. (d) Eventually, it completely fills the seed. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Development of the Seed

The mature ovule develops into the seed. A typical seed contains a seed coat, cotyledons, endosperm, and a single embryo ([link]).

Note:
Art Connection
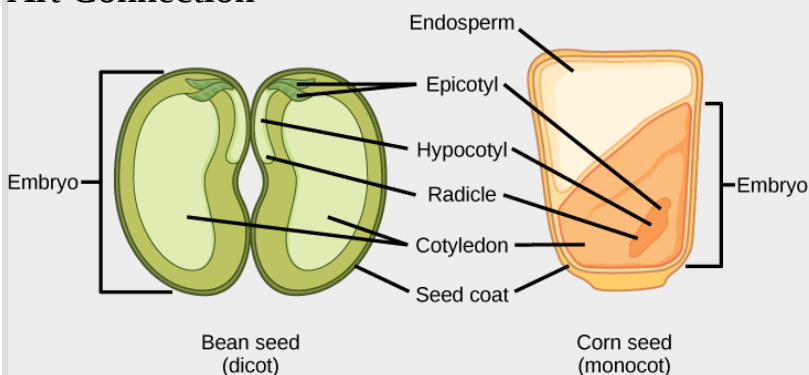
The structures of dicot and monocot seeds are shown. Dicots (left) have two cotyledons. Monocots, such as corn (right), have one cotyledon, called the scutellum; it

channels nutrition to the growing embryo. Both monocot and dicot embryos have a plumule that forms the leaves, a hypocotyl that forms the stem, and a radicle that forms the root. The embryonic axis comprises everything between the plumule and the radicle, not including the cotyledon(s).

What is of the following statements is true?

a. Both monocots and dicots have an endosperm.
b. The radicle develops into the root.
c. The plumule is part of the epicotyl
d. The endosperm is part of the embryo.

The storage of food reserves in angiosperm seeds differs between monocots and dicots. In monocots, such as corn and wheat, the single cotyledon is called a **scutellum**; the scutellum is connected directly to the embryo via vascular tissue (xylem and phloem). Food reserves are stored in the large endosperm. Upon germination, enzymes are secreted by the **aleurone**, a single layer of cells just inside the seed coat that surrounds the endosperm and embryo. The enzymes degrade the stored carbohydrates, proteins and lipids, the products of which are absorbed by the scutellum and transported via a vasculature strand to the developing embryo. Therefore, the scutellum can be seen to be an absorptive organ, not a storage organ.

The two cotyledons in the dicot seed also have vascular connections to the embryo. In **endospermic dicots**, the food reserves are stored in the endosperm. During germination, the two cotyledons therefore act as absorptive organs to take up the enzymatically released food reserves, much like in monocots (monocots, by definition, also have endospermic seeds). Tobacco (*Nicotiana tabaccum*), tomato (*Solanum lycopersicum*), and pepper (*Capsicum annuum*) are examples of endospermic dicots. In **non-endospermic dicots**, the triploid endosperm develops normally following

double fertilization, but the endosperm food reserves are quickly remobilized and moved into the developing cotyledon for storage. The two halves of a peanut seed (*Arachis hypogaea*) and the split peas (*Pisum sativum*) of split pea soup are individual cotyledons loaded with food reserves.

The seed, along with the ovule, is protected by a seed coat that is formed from the integuments of the ovule sac. In dicots, the seed coat is further divided into an outer coat known as the **testa** and inner coat known as the **tegmen**.

The embryonic axis consists of three parts: the plumule, the radicle, and the hypocotyl. The portion of the embryo between the cotyledon attachment point and the radicle is known as the **hypocotyl** (hypocotyl means "below the cotyledons"). The embryonic axis terminates in a **radicle** (the embryonic root), which is the region from which the root will develop. In dicots, the hypocotyls extend above ground, giving rise to the stem of the plant. In monocots, the hypocotyl does not show above ground because monocots do not exhibit stem elongation. The part of the embryonic axis that projects above the cotyledons is known as the **epicotyl**. The **plumule** is composed of the epicotyl, young leaves, and the shoot apical meristem.

Upon germination in dicot seeds, the epicotyl is shaped like a hook with the plumule pointing downwards. This shape is called the plumule hook, and it persists as long as germination proceeds in the dark. Therefore, as the epicotyl pushes through the tough and abrasive soil, the plumule is protected from damage. Upon exposure to light, the hypocotyl hook straightens out, the young foliage leaves face the sun and expand, and the epicotyl continues to elongate. During this time, the radicle is also growing and producing the primary root. As it grows downward to form the tap root, lateral roots branch off to all sides, producing the typical dicot tap root system.

In monocot seeds ([link]), the testa and tegmen of the seed coat are fused. As the seed germinates, the primary root emerges, protected by the root-tip covering: the **coleorhiza**. Next, the primary shoot emerges, protected by the **coleoptile**: the covering of the shoot tip. Upon exposure to light (i.e. when the plumule has exited the soil and the protective coleoptile is no longer

needed), elongation of the coleoptile ceases and the leaves expand and unfold. At the other end of the embryonic axis, the primary root soon dies, while other, adventitious roots (roots that do not arise from the usual place – i.e. the root) emerge from the base of the stem. This gives the monocot a fibrous root system.
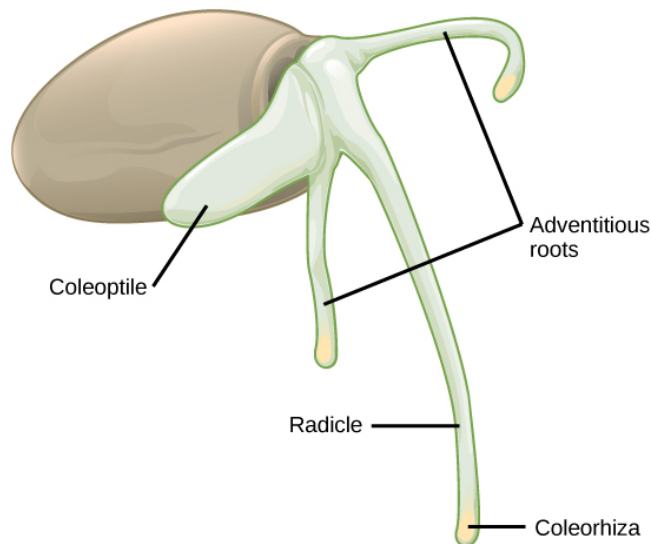
As this monocot grass seed germinates, the primary root, or radicle, emerges first, followed by the primary shoot, or coleoptile, and the adventitious roots.

Seed Germination

Many mature seeds enter a period of inactivity, or extremely low metabolic activity: a process known as **dormancy**, which may last for months, years or even centuries. Dormancy helps keep seeds viable during unfavorable conditions. Upon a return to favorable conditions, seed germination takes place. Favorable conditions could be as diverse as moisture, light, cold, fire,

or chemical treatments. After heavy rains, many new seedlings emerge. Forest fires also lead to the emergence of new seedlings. Some seeds require **vernalization** (cold treatment) before they can germinate. This guarantees that seeds produced by plants in temperate climates will not germinate until the spring. Plants growing in hot climates may have seeds that need a heat treatment in order to germinate, to avoid germination in the hot, dry summers. In many seeds, the presence of a thick seed coat retards the ability to germinate. **Scarification**, which includes mechanical or chemical processes to soften the seed coat, is often employed before germination. Presoaking in hot water, or passing through an acid environment, such as an animal's digestive tract, may also be employed.

Depending on seed size, the time taken for a seedling to emerge may vary. Species with large seeds have enough food reserves to germinate deep below ground, and still extend their epicotyl all the way to the soil surface. Seeds of small-seeded species usually require light as a germination cue. This ensures the seeds only germinate at or near the soil surface (where the light is greatest). If they were to germinate too far underneath the surface, the developing seedling would not have enough food reserves to reach the sunlight.

Development of Fruit and Fruit Types

After fertilization, the ovary of the flower usually develops into the fruit. Fruits are usually associated with having a sweet taste; however, not all fruits are sweet. Botanically, the term "fruit" is used for a ripened ovary. In most cases, flowers in which fertilization has taken place will develop into fruits, and flowers in which fertilization has not taken place will not. Some fruits develop from the ovary and are known as true fruits, whereas others develop from other parts of the female gametophyte and are known as accessory fruits. The fruit encloses the seeds and the developing embryo, thereby providing it with protection. Fruits are of many types, depending on their origin and texture. The sweet tissue of the blackberry, the red flesh of the tomato, the shell of the peanut, and the hull of corn (the tough, thin part that gets stuck in your teeth when you eat popcorn) are all fruits. As the fruit matures, the seeds also mature.

Fruits may be classified as simple, aggregate, multiple, or accessory, depending on their origin ([link]). If the fruit develops from a single carpel or fused carpels of a single ovary, it is known as a **simple fruit**, as seen in nuts and beans. An **aggregate fruit** is one that develops from more than one carpel, but all are in the same flower: the mature carpels fuse together to form the entire fruit, as seen in the raspberry. **Multiple fruit** develops from an inflorescence or a cluster of flowers. An example is the pineapple, where the flowers fuse together to form the fruit. **Accessory fruits** (sometimes called false fruits) are not derived from the ovary, but from another part of the flower, such as the receptacle (strawberry) or the hypanthium (apples and pears).

Simple fruit

Aggregate fruit
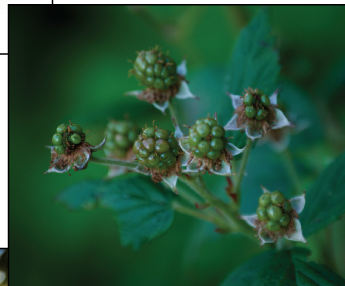
Accessory fruit

Multiple fruit

There are four main types of fruits. Simple fruits, such as these nuts, are derived from a

single ovary. Aggregate fruits, like raspberries, form from many carpels that fuse together. Multiple fruits, such as pineapple, form from a cluster of flowers called an inflorescence. Accessory fruit, like the apple, are formed from a part of the plant other than the ovary. (credit "nuts": modification of work by Petr Kratochvil; credit "raspberries": modification of work by Cory Zanker; credit "pineapple": modification of work by Howie Le; credit "apple": modification of work by Paolo Neo)

Fruits generally have three parts: the **exocarp** (the outermost skin or covering), the **mesocarp** (middle part of the fruit), and the **endocarp** (the inner part of the fruit). Together, all three are known as the **pericarp**. The mesocarp is usually the fleshy, edible part of the fruit; however, in some fruits, such as the almond, the endocarp is the edible part. In many fruits, two or all three of the layers are fused, and are indistinguishable at maturity. Fruits can be dry or fleshy. Furthermore, fruits can be divided into dehiscent or indehiscent types. Dehiscent fruits, such as peas, readily release their seeds, while indehiscent fruits, like peaches, rely on decay to release their seeds.

Fruit and Seed Dispersal

The fruit has a single purpose: seed dispersal. Seeds contained within fruits need to be dispersed far from the mother plant, so they may find favorable and less competitive conditions in which to germinate and grow.

Some fruit have built-in mechanisms so they can disperse by themselves, whereas others require the help of agents like wind, water, and animals ([link]). Modifications in seed structure, composition, and size help in dispersal. Wind-dispersed fruit are lightweight and may have wing-like

appendages that allow them to be carried by the wind. Some have a parachute-like structure to keep them afloat. Some fruits—for example, the dandelion—have hairy, weightless structures that are suited to dispersal by wind.

Seeds dispersed by water are contained in light and buoyant fruit, giving them the ability to float. Coconuts are well known for their ability to float on water to reach land where they can germinate. Similarly, willow and silver birches produce lightweight fruit that can float on water.

Animals and birds eat fruits, and the seeds that are not digested are excreted in their droppings some distance away. Some animals, like squirrels, bury seed-containing fruits for later use; if the squirrel does not find its stash of fruit, and if conditions are favorable, the seeds germinate. Some fruits, like the cocklebur, have hooks or sticky structures that stick to an animal's coat and are then transported to another place. Humans also play a big role in dispersing seeds when they carry fruits to new places and throw away the inedible part that contains the seeds.

All of the above mechanisms allow for seeds to be dispersed through space, much like an animal's offspring can move to a new location. Seed dormancy, which was described earlier, allows plants to disperse their progeny through time: something animals cannot do. Dormant seeds can wait months, years, or even decades for the proper conditions for germination and propagation of the species.

Fruits and seeds are dispersed by various means. (a) Dandelion seeds are dispersed by wind, the (b) coconut seed is dispersed by water, and the (c) acorn is dispersed by

animals that cache and then forget it.
(credit a: modification of work by
"Rosendahl"/Flickr; credit b: modification
of work by Shine Oa; credit c:
modification of work by Paolo Neo)

Section Summary

For fertilization to occur in angiosperms, pollen has to be transferred to the stigma of a flower: a process known as pollination. Gymnosperm pollination involves the transfer of pollen from a male cone to a female cone. When the pollen of the flower is transferred to the stigma of the same flower, it is called self-pollination. Cross-pollination occurs when pollen is transferred from one flower to another flower on the same plant, or another plant. Cross-pollination requires pollinating agents such as water, wind, or animals, and increases genetic diversity. After the pollen lands on the stigma, the tube cell gives rise to the pollen tube, through which the generative nucleus migrates. The pollen tube gains entry through the micropyle on the ovule sac. The generative cell divides to form two sperm cells: one fuses with the egg to form the diploid zygote, and the other fuses with the polar nuclei to form the endosperm, which is triploid in nature. This is known as double fertilization. After fertilization, the zygote divides to form the embryo and the fertilized ovule forms the seed. The walls of the ovary form the fruit in which the seeds develop. The seed, when mature, will germinate under favorable conditions and give rise to the diploid sporophyte.

Art Connections

Exercise:

Problem: [link] What is the function of the cotyledon?

    a. It develops into the root.

b. It provides nutrition for the embryo.
c. It forms the embryo.
d. It protects the embryo.

Solution:

B

Review Questions

Exercise:

Problem: After double fertilization, a zygote and _____ form.

a. an ovule
b. endosperm
c. a cotyledon
d. a suspensor

Solution:

B

Exercise:

Problem: The fertilized ovule gives rise to the _____.

a. fruit
b. seed
c. endosperm
d. embryo

Solution:

B

Exercise:

Problem:

What is the term for a fruit that develops from tissues other than the ovary?

    a. simple fruit
    b. aggregate fruit
    c. multiple fruit
    d. accessory fruit

Solution:

D

Exercise:

Problem: The _____ is the outermost covering of a fruit.

    a. endocarp
    b. pericarp
    c. exocarp
    d. mesocarp

Solution:

C

Free Response

Exercise:

Problem:

Why do some seeds undergo a period of dormancy, and how do they break dormancy?

Solution:

Many seeds enter a period of inactivity or extremely low metabolic activity, a process known as dormancy. Dormancy allows seeds to tide over unfavorable conditions and germinate on return to favorable conditions. Favorable conditions could be as diverse as moisture, light, cold, fire, or chemical treatments. After heavy rains, many new seedlings emerge. Forest fires also lead to the emergence of new seedlings.

Exercise:

Problem: Discuss some ways in which fruit seeds are dispersed.

Solution:

Some fruits have built-in mechanisms that allow them to disperse seeds by themselves, but others require the assistance of agents like wind, water, and animals. Fruit that are dispersed by the wind are light in weight and often have wing-like appendages that allow them to be carried by the wind; other have structures resembling a parachute that keep them afloat in the wind. Some fruits, such as those of dandelions, have hairy, weightless structures that allow them to float in the wind. Fruits dispersed by water are light and buoyant, giving them the ability to float; coconuts are one example. Animals and birds eat fruits and disperse their seeds by leaving droppings at distant locations. Other animals bury fruit that may later germinate. Some fruits stick to animals' bodies and are carried to new locations. People also contribute to seed dispersal when they carry fruits to new places.

Glossary

accessory fruit
    fruit derived from tissues other than the ovary

aggregate fruit
    fruit that develops from multiple carpels in the same flower

aleurone
    single layer of cells just inside the seed coat that secretes enzymes
    upon germination

coleoptile
    covering of the shoot tip, found in germinating monocot seeds

coleorhiza
    covering of the root tip, found in germinating monocot seeds

cotyledon
    fleshy part of seed that provides nutrition to the seed

cross-pollination
    transfer of pollen from the anther of one flower to the stigma of a
    different flower

dormancy
    period of no growth and very slow metabolic processes

double fertilization
    two fertilization events in angiosperms; one sperm fuses with the egg,
    forming the zygote, whereas the other sperm fuses with the polar
    nuclei, forming endosperm

endocarp
    innermost part of fruit

endosperm
    triploid structure resulting from fusion of a sperm with polar nuclei,
    which serves as a nutritive tissue for embryo

endospermic dicot

dicot that stores food reserves in the endosperm

exocarp
    outermost covering of a fruit

epicotyl
    embryonic shoot above the cotyledons

gravitropism
    response of a plant growth in the same direction as gravity

hypocotyl
    embryonic axis above the cotyledons

mesocarp
    middle part of a fruit

multiple fruit
    fruit that develops from multiple flowers on an inflorescence

nectar guide
    pigment pattern on a flower that guides an insect to the nectaries

non-endospermic dicot
    dicot that stores food reserves in the developing cotyledon

pericarp
    collective term describing the exocarp, mesocarp, and endocarp; the
    structure that encloses the seed and is a part of the fruit

plumule
    shoot that develops from the germinating seed

pollination
    transfer of pollen to the stigma

radicle
    original root that develops from the germinating seed

scarification
	mechanical or chemical processes to soften the seed coat

scutellum
	type of cotyledon found in monocots, as in grass seeds

self-pollination
	transfer of pollen from the anther to the stigma of same flower

simple fruit
	fruit that develops from a single carpel or fused carpels

suspensor
	part of the growing embryo that makes connection with the maternal tissues

tegmen
	inner layer of the seed coat

testa
	outer layer of the seed coat

vernalization
	exposure to cold required by some seeds before they can germinate

Asexual Reproduction
By the end of this section, you will be able to:

- Compare the mechanisms and methods of natural and artificial asexual reproduction
- Describe the advantages and disadvantages of natural and artificial asexual reproduction
- Discuss plant life spans

Many plants are able to propagate themselves using asexual reproduction. This method does not require the investment required to produce a flower, attract pollinators, or find a means of seed dispersal. Asexual reproduction produces plants that are genetically identical to the parent plant because no mixing of male and female gametes takes place. Traditionally, these plants survive well under stable environmental conditions when compared with plants produced from sexual reproduction because they carry genes identical to those of their parents.

Many different types of roots exhibit asexual reproduction [link]. The corm is used by gladiolus and garlic. Bulbs, such as a scaly bulb in lilies and a tunicate bulb in daffodils, are other common examples. A potato is a stem tuber, while parsnip propagates from a taproot. Ginger and iris produce rhizomes, while ivy uses an adventitious root (a root arising from a plant part other than the main or primary root), and the strawberry plant has a stolon, which is also called a runner.
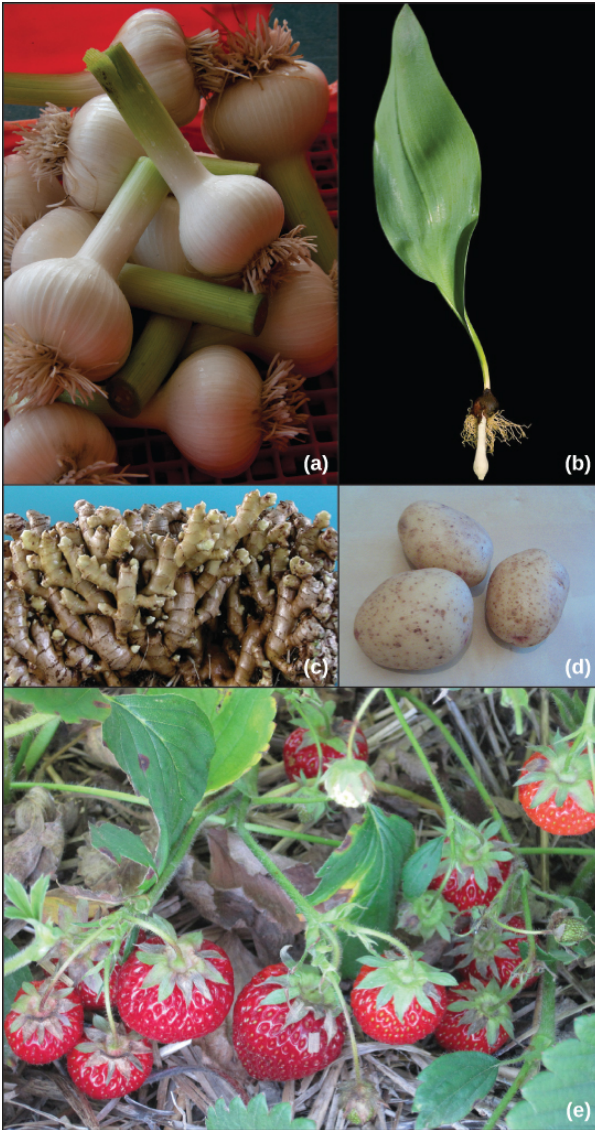
Different types of stems allow for asexual reproduction. (a) The corm of a garlic plant looks similar to (b) a tulip bulb, but the corm is solid tissue, while the bulb consists of layers of modified leaves that surround an underground stem. Both corms and bulbs can self-propagate, giving rise to new plants. (c) Ginger forms masses

of stems called rhizomes that can give rise to multiple plants. (d) Potato plants form fleshy stem tubers. Each eye in the stem tuber can give rise to a new plant. (e) Strawberry plants form stolons: stems that grow at the soil surface or just below ground and can give rise to new plants. (credit a: modification of work by Dwight Sipler; credit c: modification of work by Albert Cahalan, USDA ARS; credit d: modification of work by Richard North; credit e: modification of work by Julie Magro)

Some plants can produce seeds without fertilization. Either the ovule or part of the ovary, which is diploid in nature, gives rise to a new seed. This method of reproduction is known as **apomixis**.

An advantage of asexual reproduction is that the resulting plant will reach maturity faster. Since the new plant is arising from an adult plant or plant parts, it will also be sturdier than a seedling. Asexual reproduction can take place by natural or artificial (assisted by humans) means.

Natural Methods of Asexual Reproduction

Natural methods of asexual reproduction include strategies that plants have developed to self-propagate. Many plants—like ginger, onion, gladioli, and dahlia—continue to grow from buds that are present on the surface of the stem. In some plants, such as the sweet potato, adventitious roots or runners can give rise to new plants [link]. In *Bryophyllum* and kalanchoe, the leaves have small buds on their margins. When these are detached from the plant,

they grow into independent plants; or, they may start growing into independent plants if the leaf touches the soil. Some plants can be propagated through cuttings alone.
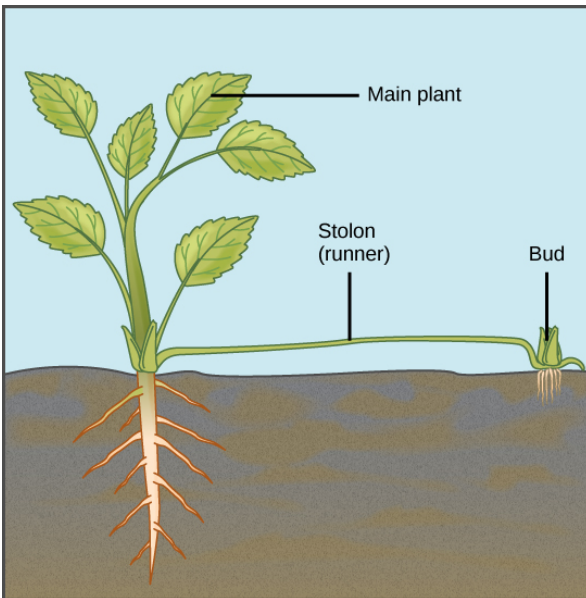
A stolon, or runner, is a stem that runs along the ground. At the nodes, it forms adventitious roots and buds that grow into a new plant.

Artificial Methods of Asexual Reproduction

These methods are frequently employed to give rise to new, and sometimes novel, plants. They include grafting, cutting, layering, and micropropagation.

Grafting

Grafting has long been used to produce novel varieties of roses, citrus species, and other plants. In **grafting**, two plant species are used; part of the stem of the desirable plant is grafted onto a rooted plant called the stock. The part that is grafted or attached is called the **scion**. Both are cut at an oblique angle (any angle other than a right angle), placed in close contact with each other, and are then held together [link]. Matching up these two surfaces as closely as possible is extremely important because these will be holding the plant together. The vascular systems of the two plants grow and fuse, forming a graft. After a period of time, the scion starts producing shoots, and eventually starts bearing flowers and fruits. Grafting is widely used in viticulture (grape growing) and the citrus industry. Scions capable of producing a particular fruit variety are grated onto root stock with specific resistance to disease.

Scion

Stock
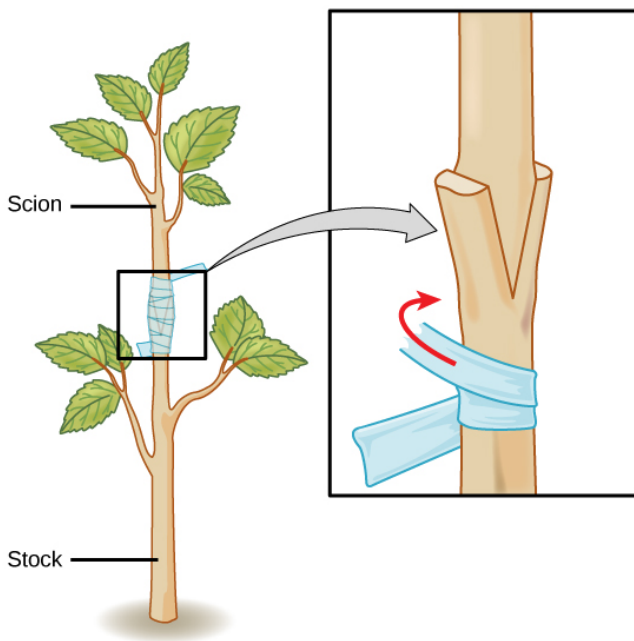
Grafting is an artificial method of asexual reproduction used to produce plants combining favorable stem characteristics with favorable root characteristics. The stem of the plant to be grafted is

known as the scion, and the root is
called the stock.

Cutting

Plants such as coleus and money plant are propagated through stem **cuttings**, where a portion of the stem containing nodes and internodes is placed in moist soil and allowed to root. In some species, stems can start producing a root even when placed only in water. For example, leaves of the African violet will root if kept in water undisturbed for several weeks.

Layering

Layering is a method in which a stem attached to the plant is bent and covered with soil. Young stems that can be bent easily without any injury are preferred. Jasmine and bougainvillea (paper flower) can be propagated this way [link]. In some plants, a modified form of layering known as air layering is employed. A portion of the bark or outermost covering of the stem is removed and covered with moss, which is then taped. Some gardeners also apply rooting hormone. After some time, roots will appear, and this portion of the plant can be removed and transplanted into a separate pot.
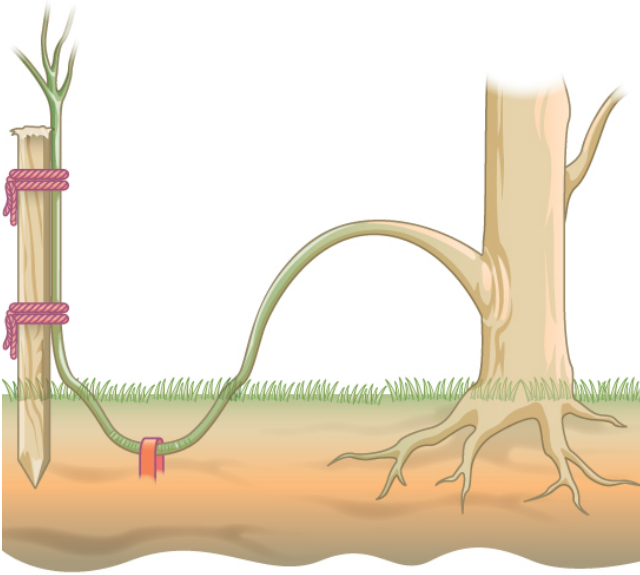
In layering, a part of the stem is buried so that it forms a new plant. (credit: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

Micropropagation

Micropropagation (also called plant tissue culture) is a method of propagating a large number of plants from a single plant in a short time under laboratory conditions [link]. This method allows propagation of rare, endangered species that may be difficult to grow under natural conditions, are economically important, or are in demand as disease-free plants.

Micropropagation is used to propagate plants in sterile conditions. (credit: Nikhilesh Sanyal)

To start plant tissue culture, a part of the plant such as a stem, leaf, embryo, anther, or seed can be used. The plant material is thoroughly sterilized using a combination of chemical treatments standardized for that species. Under sterile conditions, the plant material is placed on a plant tissue culture medium that contains all the minerals, vitamins, and hormones required by the plant. The plant part often gives rise to an undifferentiated mass known as callus, from which individual plantlets begin to grow after a period of time. These can be separated and are first grown under greenhouse conditions before they are moved to field conditions.

Plant Life Spans

The length of time from the beginning of development to the death of a plant is called its life span. The life cycle, on the other hand, is the sequence of stages a plant goes through from seed germination to seed production of the mature plant. Some plants, such as annuals, only need a few weeks to grow, produce seeds and die. Other plants, such as the bristlecone pine, live for thousands of years. Some bristlecone pines have a documented age of 4,500 years [link]. Even as some parts of a plant, such as regions containing meristematic tissue—the area of active plant growth consisting of undifferentiated cells capable of cell division—continue to grow, some parts undergo programmed cell death (apoptosis). The cork found on stems, and the water-conducting tissue of the xylem, for example, are composed of dead cells.

The bristlecone pine, shown here in the Ancient Bristlecone Pine Forest in the White Mountains of eastern California, has been known to live for 4,500 years. (credit: Rick Goldwaser)

Plant species that complete their lifecycle in one season are known as annuals, an example of which is *Arabidopsis*, or mouse-ear cress. Biennials such as carrots complete their lifecycle in two seasons. In a biennial's first

season, the plant has a vegetative phase, whereas in the next season, it completes its reproductive phase. Commercial growers harvest the carrot roots after the first year of growth, and do not allow the plants to flower. Perennials, such as the magnolia, complete their lifecycle in two years or more.

In another classification based on flowering frequency, **monocarpic** plants flower only once in their lifetime; examples include bamboo and yucca. During the vegetative period of their life cycle (which may be as long as 120 years in some bamboo species), these plants may reproduce asexually and accumulate a great deal of food material that will be required during their once-in-a-lifetime flowering and setting of seed after fertilization. Soon after flowering, these plants die. **Polycarpic** plants form flowers many times during their lifetime. Fruit trees, such as apple and orange trees, are polycarpic; they flower every year. Other polycarpic species, such as perennials, flower several times during their life span, but not each year. By this means, the plant does not require all its nutrients to be channelled towards flowering each year.

As is the case with all living organisms, genetics and environmental conditions have a role to play in determining how long a plant will live. Susceptibility to disease, changing environmental conditions, drought, cold, and competition for nutrients are some of the factors that determine the survival of a plant. Plants continue to grow, despite the presence of dead tissue such as cork. Individual parts of plants, such as flowers and leaves, have different rates of survival. In many trees, the older leaves turn yellow and eventually fall from the tree. Leaf fall is triggered by factors such as a decrease in photosynthetic efficiency, due to shading by upper leaves, or oxidative damage incurred as a result of photosynthetic reactions. The components of the part to be shed are recycled by the plant for use in other processes, such as development of seed and storage. This process is known as nutrient recycling.

The aging of a plant and all the associated processes is known as **senescence**, which is marked by several complex biochemical changes. One of the characteristics of senescence is the breakdown of chloroplasts, which is characterized by the yellowing of leaves. The chloroplasts contain

components of photosynthetic machinery such as membranes and proteins. Chloroplasts also contain DNA. The proteins, lipids, and nucleic acids are broken down by specific enzymes into smaller molecules and salvaged by the plant to support the growth of other plant tissues.

The complex pathways of nutrient recycling within a plant are not well understood. Hormones are known to play a role in senescence. Applications of cytokinins and ethylene delay or prevent senescence; in contrast, abscissic acid causes premature onset of senescence.

Sections Summary

Many plants reproduce asexually as well as sexually. In asexual reproduction, part of the parent plant is used to generate a new plant. Grafting, layering, and micropropagation are some methods used for artificial asexual reproduction. The new plant is genetically identical to the parent plant from which the stock has been taken. Asexually reproducing plants thrive well in stable environments.

Plants have different life spans, dependent on species, genotype, and environmental conditions. Parts of the plant, such as regions containing meristematic tissue, continue to grow, while other parts experience programmed cell death. Leaves that are no longer photosynthetically active are shed from the plant as part of senescence, and the nutrients from these leaves are recycled by the plant. Other factors, including the presence of hormones, are known to play a role in delaying senescence.

Review Questions

Exercise:

  Problem:

  _____ is a useful method of asexual reproduction for propagating hard-to-root plants.

      a. grafting

b. layering
c. cuttings
d. budding

Solution:

A

Exercise:

Problem:

Which of the following is an advantage of asexual reproduction?

a. Cuttings taken from an adult plant show increased resistance to diseases.
b. Grafted plants can more successfully endure drought.
c. When cuttings or buds are taken from an adult plant or plant parts, the resulting plant will grow into an adult faster than a seedling.
d. Asexual reproduction takes advantage of a more diverse gene pool.

Solution:

C

Exercise:

Problem:

Plants that flower once in their lifetime are known as _____.

a. monoecious
b. dioecious
c. polycarpic
d. monocarpic

Solution:

D

Exercise:

Problem:

Plant species that complete their lifecycle in one season are known as _____.

    a. biennials
    b. perennials
    c. annuals
    d. polycarpic

Solution:

C

Free Response

Exercise:

Problem:

What are some advantages of asexual reproduction in plants?

Solution:

Asexual reproduction does not require the expenditure of the plant's resources and energy that would be involved in producing a flower, attracting pollinators, or dispersing seeds. Asexual reproduction results in plants that are genetically identical to the parent plant, since there is no mixing of male and female gametes, resulting in better survival. The cuttings or buds taken from an adult plant produce progeny that mature faster and are sturdier than a seedling grown from a seed.

Exercise:

Problem:

Describe natural and artificial methods of asexual reproduction in plants.

Solution:

Asexual reproduction in plants can take place by natural methods or artificial methods. Natural methods include strategies used by the plant to propagate itself. Artificial methods include grafting, cutting, layering, and micropropagation.

Exercise:

Problem: Discuss the life cycles of various plants.

Solution:

Plant species that complete their life cycle in one season are known as annuals. Biennials complete their life cycle in two seasons. In the first season, the plant has a vegetative phase, whereas in the next season, it completes its reproductive phase. Perennials, such as the magnolia, complete their life cycle in two years or more.

Exercise:

Problem:

How are plants classified on the basis of flowering frequency?

Solution:

Monocarpic plants flower only once during their lifetime. During the vegetative period of their lifecycle, these plants accumulate a great deal of food material that will be required during their once-in-a-lifetime flowering and setting of seed after fertilization. Soon after flowering, these plants die. Polycarpic plants flower several times

during their life span; therefore, not all nutrients are channelled towards flowering.

Glossary

apomixis
    process by which seeds are produced without fertilization of sperm and egg

cutting
    method of asexual reproduction where a portion of the stem contains notes and internodes is placed in moist soil and allowed to root

grafting
    method of asexual reproduction where the stem from one plant species is spliced to a different plant

layering
    method of propagating plants by bending a stem under the soil

micropropagation
    propagation of desirable plants from a plant part; carried out in a laboratory

monocarpic
    plants that flower once in their lifetime

polycarpic
    plants that flower several times in their lifetime

scion
    the part of a plant that is grafted onto the root stock of another plant

senescence
    process that describes aging in plant tissues

Introduction
class="introduction"

Nearly 97 percent of animal species are invertebrates, including this sea star (*Astropecten articulates*) common to the eastern and southern coasts of the United States (credit: modification of work by Mark Walz)

A brief look at any magazine pertaining to our natural world, such as *National Geographic*, would show a rich variety of vertebrates, especially mammals and birds. To most people, these are the animals that attract our attention. Concentrating on vertebrates, however, gives us a rather biased and limited view of biodiversity, because it ignores nearly 97 percent of the animal kingdom, namely the invertebrates. Invertebrate animals are those without a cranium and defined vertebral column or spine. In addition to lacking a spine, most invertebrates also lack an endoskeleton. A large number of invertebrates are aquatic animals, and scientific research suggests that many of the world's species are aquatic invertebrates that have not yet been documented.

Features Used to Classify Animals
By the end of this section, you will be able to:

- Explain the differences in animal body plans that support basic animal classification
- Compare and contrast the embryonic development of protostomes and deuterostomes

Scientists have developed a classification scheme that categorizes all members of the animal kingdom, although there are exceptions to most "rules" governing animal classification ([link]). Animals are primarily classified according to morphological and developmental characteristics, such as a body plan. One of the most prominent features of the body plan of true animals is that they are morphologically symmetrical. This means that their distribution of body parts is balanced along an axis. Additional characteristics include the number of tissue layers formed during development, the presence or absence of an internal body cavity, and other features of embryological development, such as the origin of the mouth and anus.

Note:
Art Connection
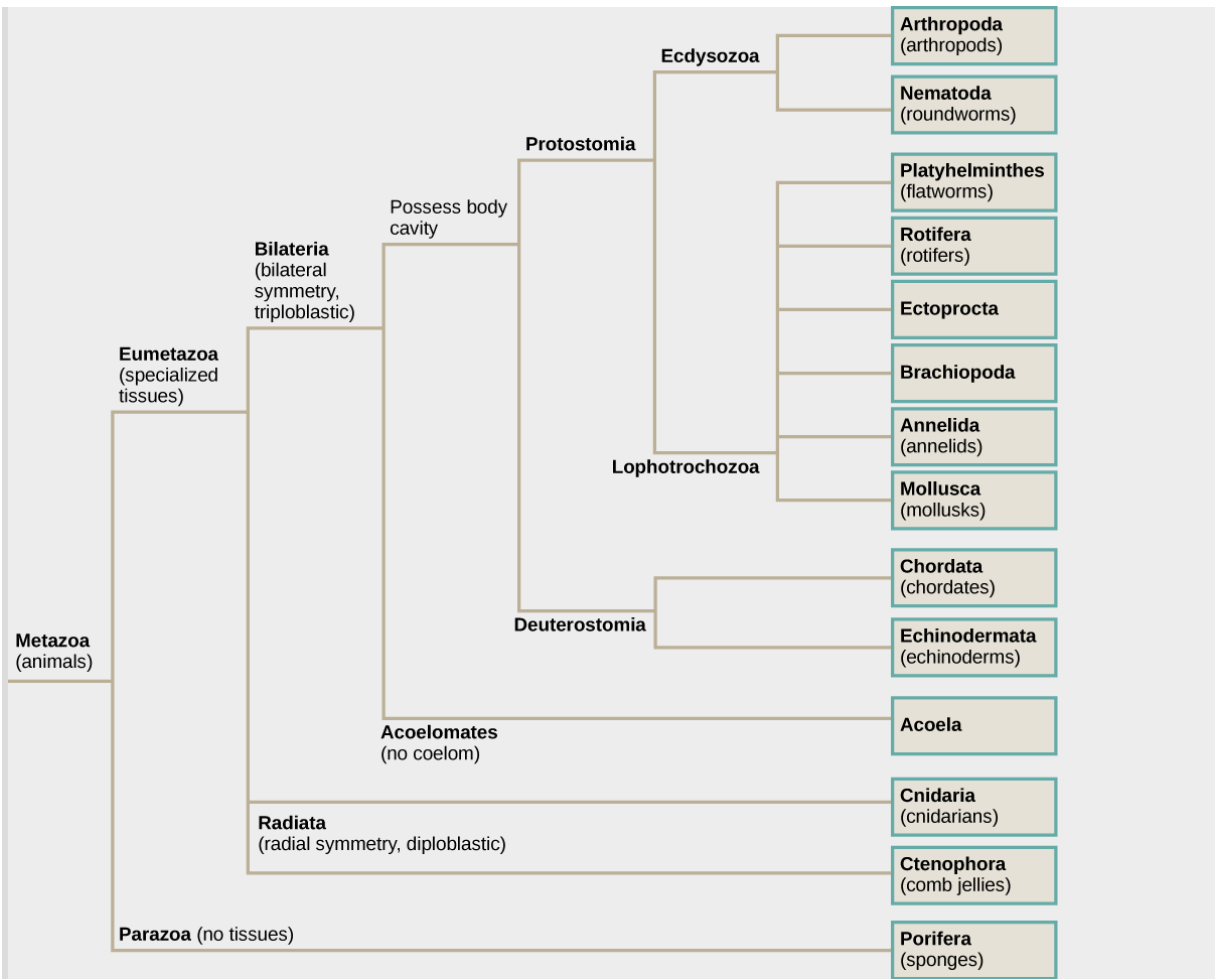
The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

Which of the following statements is false?

a. Eumetazoans have specialized tissues and parazoans don't.
b. Lophotrochozoa and Ecdysozoa are both Bilataria.
c. Acoela and Cnidaria both possess radial symmetry.
d. Arthropods are more closely related to nematodes than they are to annelids.

Animal Characterization Based on Body Symmetry

At a very basic level of classification, true animals can be largely divided into three groups based on the type of symmetry of their body plan: radially symmetrical, bilaterally symmetrical, and asymmetrical. Asymmetry is a unique feature of Parazoa ([link]**a**). Only a few animal groups display radial symmetry. All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.

Radial symmetry is the arrangement of body parts around a central axis, as is seen in a drinking glass or pie. It results in animals having top and bottom surfaces but no left and right sides, or front or back. The two halves of a radially symmetrical animal may be described as the side with a mouth or "oral side," and the side without a mouth (the "aboral side"). This form of symmetry marks the body plans of animals in the phyla Ctenophora and Cnidaria, including jellyfish and adult sea anemones ([link]**bc**). Radial symmetry equips these sea creatures (which may be sedentary or only capable of slow movement or floating) to experience the environment equally from all directions.

(a)
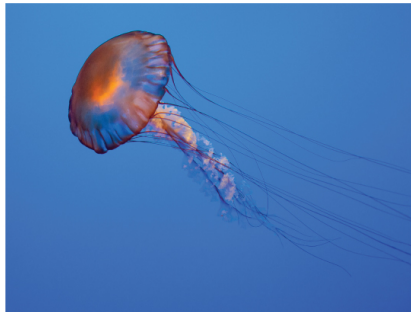
(b)

(c)
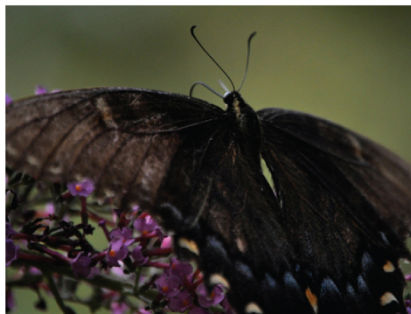
(d)

The (a) sponge is asymmetrical. The (b) jellyfish and (c) anemone are radially symmetrical, and the (d) butterfly is bilaterally symmetrical. (credit a: modification of work by Andrew Turner; credit b: modification of work by Robert Freiburger; credit c: modification of work by Samuel Chow; credit d: modification of work by Cory Zanker)

Bilateral symmetry involves the division of the animal through a sagittal plane, resulting in two mirror image, right and left halves, such as those of a butterfly ([link]**d**), crab, or human body. Animals with bilateral symmetry have a "head" and "tail" (anterior vs. posterior), front and back (dorsal vs. ventral), and right and left sides ([link]). All true animals except those with radial symmetry are bilaterally symmetrical. The evolution of bilateral symmetry that allowed for the formation of anterior and posterior (head and tail) ends promoted a phenomenon called cephalization, which refers to the collection of an organized nervous system at the animal's anterior end. In contrast to radial symmetry, which is best suited for stationary or limited-motion lifestyles, bilateral symmetry allows for streamlined and directional motion. In evolutionary terms, this simple form of symmetry promoted active mobility and increased sophistication of resource-seeking and predator-prey relationships.
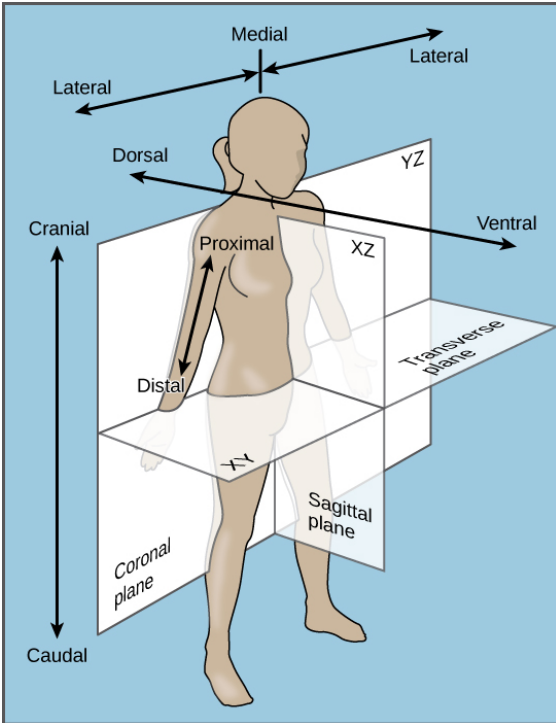
The bilaterally symmetrical human body can be divided into planes.

Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display radial symmetry as adults, but their larval stages exhibit bilateral symmetry. This is termed secondary radial symmetry. They are believed to have evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.

Note:
Link to Learning

Watch this video to see a quick sketch of the different types of body symmetry.
https://www.openstaxcollege.org/l/symmetry

Animal Characterization Based on Features of Embryological Development

Most animal species undergo a separation of tissues into germ layers during embryonic development. Recall that these germ layers are formed during gastrulation, and that they are predetermined to develop into the animal's specialized tissues and organs. Animals develop either two or three embryonic germs layers ([link]). The animals that display radial symmetry develop two germ layers, an inner layer (endoderm) and an outer layer (ectoderm). These animals are called **diploblasts**. Diploblasts have a non-living layer between the endoderm and ectoderm. More complex animals (those with bilateral symmetry) develop three tissue layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm). Animals with three tissue layers are called **triploblasts**.

Note:
Art Connection

Diploblast **Triploblast**

Endoderm

Non-living layer
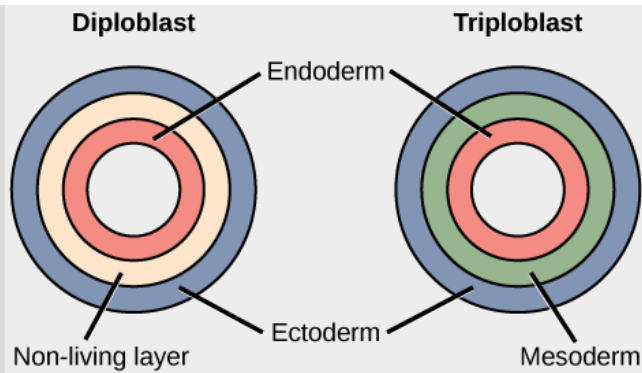
Ectoderm

Mesoderm

During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

Which of the following statements about diploblasts and triploblasts is false?

a. Animals that display radial symmetry are diploblasts.
b. Animals that display bilateral symmetry are triploblasts.
c. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
d. The mesoderm gives rise to the central nervous system.

Each of the three germ layers is programmed to give rise to particular body tissues and organs. The endoderm gives rise to the lining of the digestive tract (including the stomach, intestines, liver, and pancreas), as well as to the lining of the trachea, bronchi, and lungs of the respiratory tract, along with a few other structures. The ectoderm develops into the outer epithelial covering of the body surface, the central nervous system, and a few other structures. The mesoderm is the third germ layer; it forms between the

endoderm and ectoderm in triploblasts. This germ layer gives rise to all muscle tissues (including the cardiac tissues and muscles of the intestines), connective tissues such as the skeleton and blood cells, and most other visceral organs such as the kidneys and the spleen.

Presence or Absence of a Coelom

Further subdivision of animals with three germ layers (triploblasts) results in the separation of animals that may develop an internal body cavity derived from mesoderm, called a **coelom**, and those that do not. This epithelial cell-lined coelomic cavity represents a space, usually filled with fluid, which lies between the visceral organs and the body wall. It houses many organs such as the digestive system, kidneys, reproductive organs, and heart, and contains the circulatory system. In some animals, such as mammals, the part of the coelom called the pleural cavity provides space for the lungs to expand during breathing. The evolution of the coelom is associated with many functional advantages. Primarily, the coelom provides cushioning and shock absorption for the major organ systems. Organs housed within the coelom can grow and move freely, which promotes optimal organ development and placement. The coelom also provides space for the diffusion of gases and nutrients, as well as body flexibility, promoting improved animal motility.

Triploblasts that do not develop a coelom are called **acoelomates**, and their mesoderm region is completely filled with tissue, although they do still have a gut cavity. Examples of acoelomates include animals in the phylum Platyhelminthes, also known as flatworms. Animals with a true coelom are called **eucoelomates** (or coelomates) ([link]). A true coelom arises entirely within the mesoderm germ layer and is lined by an epithelial membrane. This membrane also lines the organs within the coelom, connecting and holding them in position while allowing them some free motion. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. A third group of triploblasts has a slightly different coelom derived partly from mesoderm and partly from endoderm, which is found between the two layers. Although still functional, these are considered false coeloms, and those animals are called **pseudocoelomates**. The phylum Nematoda

(roundworms) is an example of a pseudocoelomate. True coelomates can be further characterized based on certain features of their early embryological development.

Flatworm: *Pseudobiceros bedfordi* Annelid: *Glycera* Nematode: *Heterodera glycines*
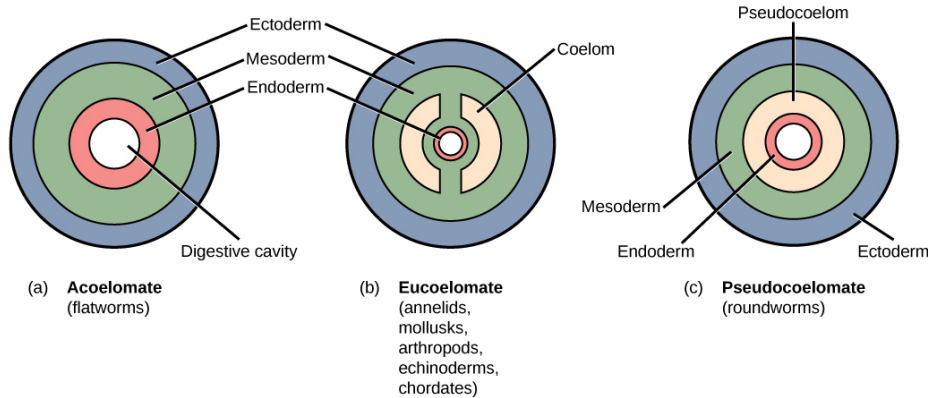
Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm. Pseudocoelomates also have a body cavity, but it is sandwiched between the endoderm and mesoderm. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS)

Embryonic Development of the Mouth

Bilaterally symmetrical, triploblastic eucoelomates can be further divided into two groups based on differences in their early embryonic development. **Protostomes** include arthropods, mollusks, and annelids. **Deuterostomes** include more complex animals such as chordates but also some simple animals such as echinoderms. These two groups are separated based on which opening of the digestive cavity develops first: mouth or anus. The word protostome comes from the Greek word meaning "mouth first," and deuterostome originates from the word meaning "mouth second" (in this case, the anus develops first). The mouth or anus develops from a structure called the blastopore ([link]). The **blastopore** is the indentation formed during the initial stages of gastrulation. In later stages, a second opening forms, and these two openings will eventually give rise to the mouth and anus ([link]). It has long been believed that the blastopore develops into the mouth of protostomes, with the second opening developing into the anus; the opposite is true for deuterostomes. Recent evidence has challenged this view of the development of the blastopore of protostomes, however, and the theory remains under debate.

Another distinction between protostomes and deuterostomes is the method of coelom formation, beginning from the gastrula stage. The coelom of most protostomes is formed through a process called **schizocoely**, meaning that during development, a solid mass of the mesoderm splits apart and forms the hollow opening of the coelom. Deuterostomes differ in that their coelom forms through a process called **enterocoely**. Here, the mesoderm develops as pouches that are pinched off from the endoderm tissue. These pouches eventually fuse to form the mesoderm, which then gives rise to the coelom.

The earliest distinction between protostomes and deuterostomes is the type of cleavage undergone by the zygote. Protostomes undergo **spiral cleavage**, meaning that the cells of one pole of the embryo are rotated, and thus misaligned, with respect to the cells of the opposite pole. This is due to the oblique angle of the cleavage. Deuterostomes undergo **radial cleavage**, where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the alignment of the cells between the two poles.

Protostomes | Deuterostomes

Blastopore
Coelom
Gastrula
Mesoderm
Mouth | Anus
Digestive tube
Anus | Mouth
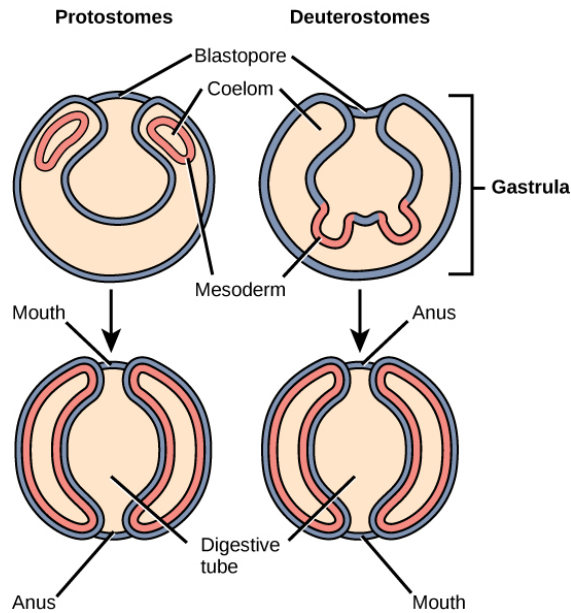
Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely. It was long believed that the blastopore developed into the mouth in protostomes and into the anus in deuterostomes, but recent evidence challenges this belief.

There is a second distinction between the types of cleavage in protostomes and deuterostomes. In addition to spiral cleavage, protostomes also undergo

determinate cleavage. This means that even at this early stage, the developmental fate of each embryonic cell is already determined. A cell does not have the ability to develop into any cell type. In contrast, deuterostomes undergo **indeterminate cleavage**, in which cells are not yet pre-determined at this early stage to develop into specific cell types. These cells are referred to as undifferentiated cells. This characteristic of deuterostomes is reflected in the existence of familiar embryonic stem cells, which have the ability to develop into any cell type until their fate is programmed at a later developmental stage.

Note:
Evolution Connection
The Evolution of the Coelom
One of the first steps in the classification of animals is to examine the animal's body. Studying the body parts tells us not only the roles of the organs in question but also how the species may have evolved. One such structure that is used in classification of animals is the coelom. A coelom is a body cavity that forms during early embryonic development. The coelom allows for compartmentalization of the body parts, so that different organ systems can evolve and nutrient transport is possible. Additionally, because the coelom is a fluid-filled cavity, it protects the organs from shock and compression. Simple animals, such as worms and jellyfish, do not have a coelom. All vertebrates have a coelom that helped them evolve complex organ systems.
Animals that do not have a coelom are called acoelomates. Flatworms and tapeworms are examples of acoelomates. They rely on passive diffusion for nutrient transport across their body. Additionally, the internal organs of acoelomates are not protected from crushing.
Animals that have a true coelom are called eucoelomates; all vertebrates are eucoelomates. The coelom evolves from the mesoderm during embryogenesis. The abdominal cavity contains the stomach, liver, gall bladder, and other digestive organs. Another category of invertebrates animals based on body cavity is pseudocoelomates. These animals have a pseudo-cavity that is not completely lined by mesoderm. Examples include nematode parasites and small worms. These animals are thought to have

evolved from coelomates and may have lost their ability to form a coelom through genetic mutations. Thus, this step in early embryogenesis—the formation of the coelom—has had a large evolutionary impact on the various species of the animal kingdom.

Section Summary

Organisms in the animal kingdom are classified based on their body morphology and development. True animals are divided into those with radial versus bilateral symmetry. Generally, the simpler and often non-motile animals display radial symmetry. Animals with radial symmetry are also generally characterized by the development of two embryological germ layers, the endoderm and ectoderm, whereas animals with bilateral symmetry are generally characterized by the development of a third embryological germ layer, the mesoderm. Animals with three germ layers, called triploblasts, are further characterized by the presence or absence of an internal body cavity called a coelom. The presence of a coelom affords many advantages, and animals with a coelom may be termed true coelomates or pseudocoelomates, depending on which tissue gives rise to the coelom. Coelomates are further divided into one of two groups called protostomes and deuterostomes, based on a number of developmental characteristics, including differences in zygote cleavage and method of coelom formation.

Art Connections

Exercise:

Problem: [link] Which of the following statements is false?

a. Eumetazoans have specialized tissues and parazoans don't.
b. Lophotrochozoa and Ecdysozoa are both Bilataria.
c. Acoela and Cnidaria both possess radial symmetry.
d. Arthropods are more closely related to nematodes than they are to annelids.

Solution:

[link] C

Exercise:

Problem:

[link] Which of the following statements about diploblasts and triploblasts is false?

a. Animals that display radial symmetry are diploblasts.
b. Animals that display bilateral symmetry are triploblasts.
c. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
d. The mesoderm gives rise to the central nervous system.

Solution:

[link] D

Review Questions

Exercise:

Problem:

Which of the following organism is most likely to be a diploblast?

a. sea star
b. shrimp
c. jellyfish
d. insect

Solution:

C

Exercise:

Problem: Which of the following is not possible?

a. radially symmetrical diploblast
b. diploblastic eucoelomate
c. protostomic coelomate
d. bilaterally symmetrical deuterostome

Solution:

B

Exercise:

Problem:

An animal whose development is marked by radial cleavage and enterocoely is _____.

a. a deuterostome
b. an annelid or mollusk
c. either an acoelomate or eucoelomate
d. none of the above

Solution:

A

Free Response

Exercise:

Problem:

Using the following terms, explain what classifications and groups humans fall into, from the most general to the most specific: symmetry, germ layers, coelom, cleavage, embryological development.

Solution:

Humans have body plans that are bilaterally symmetrical and are characterized by the development of three germ layers, making them triploblasts. Humans have true coeloms and are thus eucoelomates. As deuterostomes, humans are characterized by radial and indeterminate cleavage.

Exercise:

Problem:

Explain some of the advantages brought about through the evolution of bilateral symmetry and coelom formation.

Solution:

The evolution of bilateral symmetry led to designated head and tail body regions, and promoted more efficient mobility for animals. This improved mobility allowed for more skillful seeking of resources and prey escaping from predators. The appearance of the coelom in coelomates provides many internal organs with shock absorption, making them less prone to physical damage from bodily assault. A coelom also gives the body greater flexibility, which promotes more efficient movement. The relatively loose placement of organs within the coelom allows them to develop and grow with some spatial freedom, which promoted the evolution of optimal organ arrangement. The coelom also provides space for a circulatory system, which is an advantageous way to distribute body fluids and gases.

Glossary

acoelomate
> animal without a body cavity

bilateral symmetry
> type of symmetry in which there is only one plane of symmetry, so the left and right halves of an animal are mirror images

blastopore
> indentation formed during gastrulation, evident in the gastrula stage

coelom
> lined body cavity

determinate cleavage
> developmental tissue fate of each embryonic cell is already determined

deuterostome
> blastopore develops into the anus, with the second opening developing into the mouth

diploblast
> animal that develops from two germ layers

enterocoely
> mesoderm of deuterostomes develops as pouches that are pinched off from endodermal tissue, cavity contained within the pouches becomes coelom

eucoelomate
> animal with a body cavity completely lined with mesodermal tissue

indeterminate cleavage
> early stage of development when germ cells or "stem cells" are not yet pre-determined to develop into specific cell types

protostome
> blastopore develops into the mouth of protostomes, with the second opening developing into the anus

pseudocoelomate
    animal with a body cavity located between the mesoderm and
    endoderm

radial cleavage
    cleavage axes are parallel or perpendicular to the polar axis, resulting
    in the alignment of cells between the two poles

radial symmetry
    type of symmetry with multiple planes of symmetry, with body parts
    (rays) arranged around a central disk

schizocoely
    during development of protostomes, a solid mass of mesoderm splits
    apart and forms the hollow opening of the coelom

spiral cleavage
    cells of one pole of the embryo are rotated or misaligned with respect
    to the cells of the opposite pole

triploblast
    animal that develops from three germ layers

Phylum Porifera
By the end of this section, you will be able to:

- Describe the organizational features of the simplest multicellular organisms
- Explain the various body forms and bodily functions of sponges

The invertebrates, or **invertebrata**, are animals that do not contain bony structures, such as the cranium and vertebrae. The simplest of all the invertebrates are the Parazoans, which include only the phylum **Porifera**: the sponges ([link]). Parazoans ("beside animals") do not display tissue-level organization, although they do have specialized cells that perform specific functions. Sponge larvae are able to swim; however, adults are non-motile and spend their life attached to a substratum. Since water is vital to sponges for excretion, feeding, and gas exchange, their body structure facilitates the movement of water through the sponge. Structures such as canals, chambers, and cavities enable water to move through the sponge to nearly all body cells.

Sponges are members of the
Phylum Porifera, which contains
the simplest invertebrates. (credit:
Andrew Turner)

Morphology of Sponges

The morphology of the simplest sponges takes the shape of a cylinder with a large central cavity, the **spongocoel**, occupying the inside of the cylinder. Water can enter into the spongocoel from numerous pores in the body wall. Water entering the spongocoel is extruded via a large common opening called the **osculum**. However, sponges exhibit a range of diversity in body forms, including variations in the size of the spongocoel, the number of osculi, and where the cells that filter food from the water are located.

While sponges (excluding the hexactinellids) do not exhibit tissue-layer organization, they do have different cell types that perform distinct functions. **Pinacocytes**, which are epithelial-like cells, form the outermost layer of sponges and enclose a jelly-like substance called mesohyl. **Mesohyl** is an extracellular matrix consisting of a collagen-like gel with suspended cells that perform various functions. The gel-like consistency of mesohyl acts like an endoskeleton and maintains the tubular morphology of sponges. In addition to the osculum, sponges have multiple pores called **ostia** on their bodies that allow water to enter the sponge. In some sponges, ostia are formed by porocytes, single tube-shaped cells that act as valves to regulate the flow of water into the spongocoel. In other sponges, ostia are formed by folds in the body wall of the sponge.

Choanocytes ("collar cells") are present at various locations, depending on the type of sponge, but they always line the inner portions of some space through which water flows (the spongocoel in simple sponges, canals within the body wall in more complex sponges, and chambers scattered throughout the body in the most complex sponges). Whereas pinacocytes line the outside of the sponge, choanocytes tend to line certain inner portions of the sponge body that surround the mesohyl. The structure of a choanocyte is critical to its function, which is to generate a water current through the sponge and to trap and ingest food particles by phagocytosis. Note the similarity in appearance between the sponge choanocyte and choanoflagellates (Protista). This similarity suggests that sponges and choanoflagellates are closely related and likely share a recent common ancestry. The cell body is embedded in mesohyl and contains all organelles required for normal cell function, but protruding into the "open space"

inside of the sponge is a mesh-like collar composed of microvilli with a single flagellum in the center of the column. The cumulative effect of the flagella from all choanocytes aids the movement of water through the sponge: drawing water into the sponge through the numerous ostia, into the spaces lined by choanocytes, and eventually out through the osculum (or osculi). In the meantime, food particles, including waterborne bacteria and algae, are trapped by the sieve-like collar of the choanocytes, slide down into the body of the cell, are ingested by phagocytosis, and become encased in a food vacuole. Lastly, choanocytes will differentiate into sperm for sexual reproduction, where they will become dislodged from the mesohyl and leave the sponge with expelled water through the osculum.

Note:
Link to Learning

Watch this video to see the movement of water through the sponge body.
https://www.openstaxcollege.org/l/filter_sponges

The second crucial cells in sponges are called **amoebocytes** (or archaeocytes), named for the fact that they move throughout the mesohyl in an amoeba-like fashion. Amoebocytes have a variety of functions: delivering nutrients from choanocytes to other cells within the sponge, giving rise to eggs for sexual reproduction (which remain in the mesohyl), delivering phagocytized sperm from choanocytes to eggs, and differentiating into more-specific cell types. Some of these more-specific cell types include collencytes and lophocytes, which produce the collagen-like protein to maintain the mesohyl, sclerocytes, which produce spicules in some sponges, and spongocytes, which produce the protein spongin in the

majority of sponges. These cells produce collagen to maintain the consistency of the mesohyl. The different cell types in sponges are shown in [link].

Lophocyte or collenocyte secretes collagen.

Pinacocyte forms the outer covering of the sponge; may phagocytize large food particles.

Oocyte egg cell

Porocyte controls water flow through ostia.

Amoebocyte delivers nutrients to cells, and differentiates into other cell types.

Sclerocyte secretes silica spicules.

Choanocyte generates water current and filters food particles from water.

Osculum

Ostia

Spongocoel

Mesohyl

(a) Basic sponge body plan

(b) Some sponge cell types

The sponge's (a) basic body plan and (b) some of the specialized cell types found in sponges are shown.

Which of the following statements is false?

a. Choanocytes have flagella that propel water through the body.
b. Pinacocytes can transform into any cell type.
c. Lophocytes secrete collagen.
d. Porocytes control the flow of water through pores in the sponge body.

In some sponges, **sclerocytes** secrete small **spicules** into the mesohyl, which are composed of either calcium carbonate or silica, depending on the type of sponge. These spicules serve to provide additional stiffness to the body of the sponge. Additionally, spicules, when present externally, may ward off predators. Another type of protein, spongin, may also be present in the mesohyl of some sponges.

The presence and composition of spicules/spongin are the differentiating characteristics of the three classes of sponges ([link]): Class Calcarea contains calcium carbonate spicules and no spongin, class Hexactinellida contains six-rayed siliceous spicules and no spongin, and class Demospongia contains spongin and may or may not have spicules; if present, those spicules are siliceous. Spicules are most conspicuously present in class Hexactinellida, the order consisting of glass sponges. Some of the spicules may attain giant proportions (in relation to the typical size range of glass sponges of 3 to 10 mm) as seen in *Monorhaphis chuni*, which grows up to 3 m long.
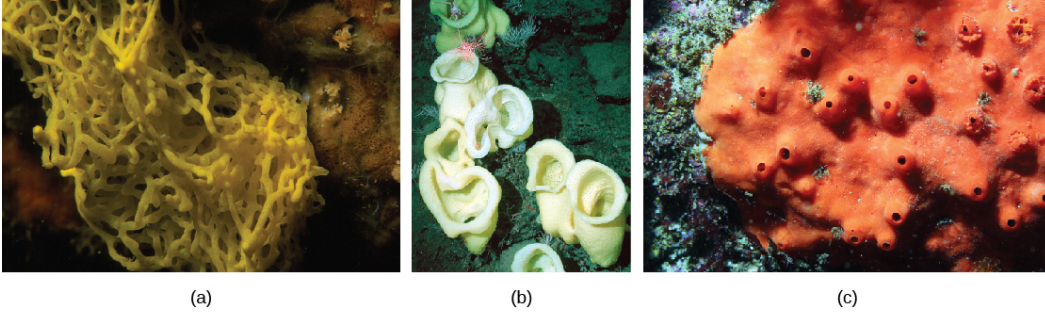
(a) *Clathrina clathrus* belongs to class Calcarea, (b) *Staurocalyptus* spp. (common name: yellow Picasso sponge) belongs to class Hexactinellida, and (c) *Acarnus erithacus* belongs to class Demospongia. (credit a: modification of work by Parent Géry; credit b: modification of work by Monterey Bay Aquarium Research Institute, NOAA; credit c: modification of work by Sanctuary Integrated Monitoring Network, Monterey Bay National Marine Sanctuary, NOAA)

Physiological Processes in Sponges

Sponges, despite being simple organisms, regulate their different physiological processes through a variety of mechanisms. These processes regulate their metabolism, reproduction, and locomotion.

Digestion

Sponges lack complex digestive, respiratory, circulatory, reproductive, and nervous systems. Their food is trapped when water passes through the ostia and out through the osculum. Bacteria smaller than 0.5 microns in size are trapped by choanocytes, which are the principal cells engaged in nutrition, and are ingested by phagocytosis. Particles that are larger than the ostia may be phagocytized by pinacocytes. In some sponges, amoebocytes transport food from cells that have ingested food particles to those that do not. For this type of digestion, in which food particles are digested within individual cells, the sponge draws water through diffusion. The limit of this type of digestion is that food particles must be smaller than individual cells.

All other major body functions in the sponge (gas exchange, circulation, excretion) are performed by diffusion between the cells that line the openings within the sponge and the water that is passing through those openings. All cell types within the sponge obtain oxygen from water through diffusion. Likewise, carbon dioxide is released into seawater by diffusion. In addition, nitrogenous waste produced as a byproduct of protein metabolism is excreted via diffusion by individual cells into the water as it passes through the sponge.

Reproduction

Sponges reproduce by sexual as well as asexual methods. The typical means of asexual reproduction is either fragmentation (where a piece of the sponge breaks off, settles on a new substrate, and develops into a new individual) or budding (a genetically identical outgrowth grows from the parent and eventually detaches or remains attached to form a colony). An atypical type of asexual reproduction is found only in freshwater sponges

and occurs through the formation of gemmules. **Gemmules** are environmentally resistant structures produced by adult sponges wherein the typical sponge morphology is inverted. In gemmules, an inner layer of amoebocytes is surrounded by a layer of collagen (spongin) that may be reinforced by spicules. The collagen that is normally found in the mesohyl becomes the outer protective layer. In freshwater sponges, gemmules may survive hostile environmental conditions like changes in temperature and serve to recolonize the habitat once environmental conditions stabilize. Gemmules are capable of attaching to a substratum and generating a new sponge. Since gemmules can withstand harsh environments, are resistant to desiccation, and remain dormant for long periods, they are an excellent means of colonization for a sessile organism.

Sexual reproduction in sponges occurs when gametes are generated. Sponges are monoecious (hermaphroditic), which means that one individual can produce both gametes (eggs and sperm) simultaneously. In some sponges, production of gametes may occur throughout the year, whereas other sponges may show sexual cycles depending upon water temperature. Sponges may also become sequentially hermaphroditic, producing oocytes first and spermatozoa later. Oocytes arise by the differentiation of amoebocytes and are retained within the spongocoel, whereas spermatozoa result from the differentiation of choanocytes and are ejected via the osculum. Ejection of spermatozoa may be a timed and coordinated event, as seen in certain species. Spermatozoa carried along by water currents can fertilize the oocytes borne in the mesohyl of other sponges. Early larval development occurs within the sponge, and free-swimming larvae are then released via the osculum.

Locomotion

Sponges are generally sessile as adults and spend their lives attached to a fixed substratum. They do not show movement over large distances like other free-swimming marine invertebrates. However, sponge cells are capable of creeping along substrata via organizational plasticity. Under experimental conditions, researchers have shown that sponge cells spread on a physical support demonstrate a leading edge for directed movement. It

has been speculated that this localized creeping movement may help sponges adjust to microenvironments near the point of attachment. It must be noted, however, that this pattern of movement has been documented in laboratories, but it remains to be observed in natural sponge habitats.

Section Summary

Animals included in phylum Porifera are Parazoans because they do not show the formation of true tissues (except in class Hexactinellida). These organisms show very simple organization, with a rudimentary endoskeleton. Sponges have multiple cell types that are geared toward executing various metabolic functions. Although these animals are very simple, they perform several complex physiological functions.

Art Connections

Exercise:

Problem: [link] Which of the following statements is false?

a. Choanocytes have flagella that propel water through the body.

b. Pinacocytes can transform into any cell type.

c. Lophocytes secrete collagen.

d. Porocytes control the flow of water through pores in the sponge body.

Solution:

[link] B

Review Questions

Exercise:

Problem: Mesohyl contains:

a. a polysaccharide gel and dead cells

b. a collagen-like gel and suspended cells for various functions

c. spicules composed of silica or calcium carbonate

d. multiple pores

Solution:

B

Exercise:

Problem: The large central opening in the Parazoan body is called the:

a. gemmule

b. spicule

c. ostia

d. osculum

Solution:

D

Free Response

Exercise:

Problem:

Describe the different cell types and their functions in sponges.

Solution:

Pinacocytes are epithelial-like cells, form the outermost layer of sponges, and enclose a jelly-like substance called mesohyl. In some sponges, porocytes form ostia, single tube-shaped cells that act as valves to regulate the flow of water into the spongocoel. Choanocytes ("collar cells") are present at various locations, depending on the type of sponge, but they always line some space through which water flows and are used in feeding.

Exercise:

Problem:

Describe the feeding mechanism of sponges and identify how it is different from other animals.

Solution:

The sponges draw water carrying food particles into the spongocoel using the beating of flagella on the choanocytes. The food particles are caught by the collar of the choanocyte and are brought into the cell by phagocytosis. Digestion of the food particle takes place inside the cell. The difference between this and the mechanisms of other animals is that digestion takes place within cells rather than outside of cells. It means that the organism can feed only on particles smaller than the cells themselves.

Glossary

amoebocyte
> sponge cell with multiple functions, including nutrient delivery, egg formation, sperm delivery, and cell differentiation

choanocyte
> (also, collar cell) sponge cell that functions to generate a water current and to trap and ingest food particles via phagocytosis

gemmule
> structure produced by asexual reproduction in freshwater sponges where the morphology is inverted

invertebrata
> (also, invertebrates) category of animals that do not possess a cranium or vertebral column

mesohyl
> collagen-like gel containing suspended cells that perform various functions in the sponge

osculum
> large opening in the sponge's body through which water leaves

ostium
> pore present on the sponge's body through which water enters

pinacocyte
> epithelial-like cell that forms the outermost layer of sponges and encloses a jelly-like substance called mesohyl

Porifera
> phylum of animals with no true tissues, but a porous body with rudimentary endoskeleton

sclerocyte
> cell that secretes silica spicules into the mesohyl

spicule
> structure made of silica or calcium carbonate that provides structural support for sponges

spongocoel
> central cavity within the body of some sponges

Phylum Cnidaria
By the end of this section, you will be able to:

- Compare structural and organization characteristics of Porifera and
  Cnidaria
- Describe the progressive development of tissues and their relevance to
  animal complexity

Phylum **Cnidaria** includes animals that show radial or biradial symmetry
and are diploblastic, that is, they develop from two embryonic layers.
Nearly all (about 99 percent) cnidarians are marine species.

Cnidarians contain specialized cells known as **cnidocytes** ("stinging cells")
containing organelles called **nematocysts** (stingers). These cells are present
around the mouth and tentacles, and serve to immobilize prey with toxins
contained within the cells. Nematocysts contain coiled threads that may
bear barbs. The outer wall of the cell has hairlike projections called
cnidocils, which are sensitive to touch. When touched, the cells are known
to fire coiled threads that can either penetrate the flesh of the prey or
predators of cnidarians (see [link]) or ensnare it. These coiled threads
release toxins into the target and can often immobilize prey or scare away
predators.
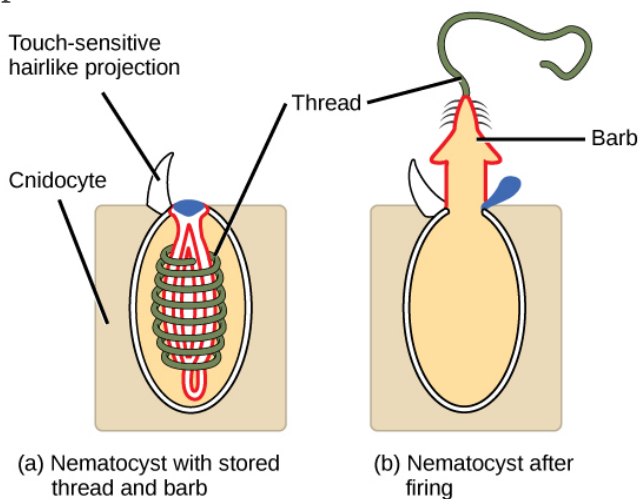
Animals from the phylum
Cnidaria have stinging cells called
cnidocytes. Cnidocytes contain
large organelles called (a)

nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

Animals in this phylum display two distinct morphological body plans: **polyp** or "stalk" and **medusa** or "bell" ([link]). An example of the polyp form is *Hydra* spp.; perhaps the most well-known medusoid animals are the jellies (jellyfish). Polyp forms are sessile as adults, with a single opening to the digestive system (the mouth) facing up with tentacles surrounding it. Medusa forms are motile, with the mouth and tentacles hanging down from an umbrella-shaped bell.
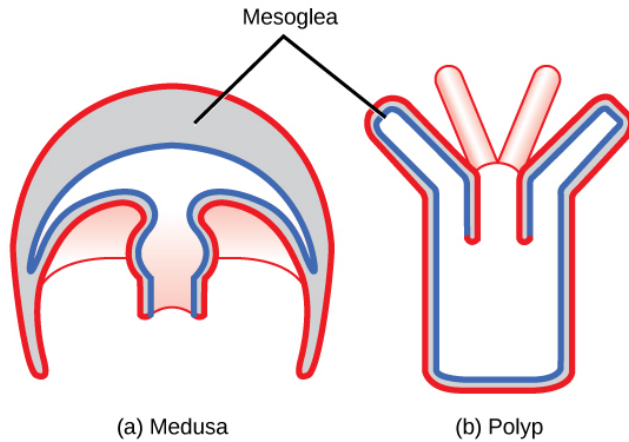
Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Some cnidarians are polymorphic, that is, they have two body plans during their life cycle. An example is the colonial hydroid called an *Obelia*. The sessile polyp form has, in fact, two types of polyps, shown in [link]. The first is the gastrozooid, which is adapted for capturing prey and feeding; the other type of polyp is the gonozooid, adapted for the asexual budding of medusa. When the reproductive buds mature, they break off and become free-swimming medusa, which are either male or female (dioecious). The male medusa makes sperm, whereas the female medusa makes eggs. After fertilization, the zygote develops into a blastula, which develops into a planula larva. The larva is free swimming for a while, but eventually attaches and a new colonial reproductive polyp is formed.
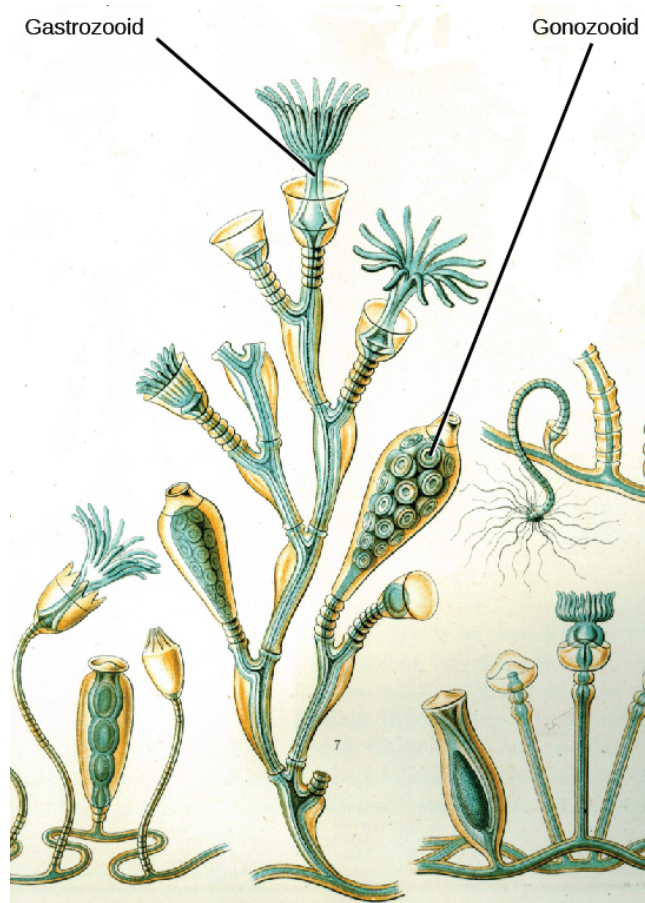
The sessile form of *Obelia geniculate* has two types of polyps: gastrozooids, which are adapted for capturing prey, and gonozooids, which bud to produce medusae asexually.

Note:
Link to Learning

All cnidarians show the presence of two membrane layers in the body that are derived from the endoderm and ectoderm of the embryo. The outer layer (from ectoderm) is called the **epidermis** and lines the outside of the animal, whereas the inner layer (from endoderm) is called the **gastrodermis** and lines the digestive cavity. Between these two membrane layers is a non-living, jelly-like **mesoglea** connective layer. In terms of cellular complexity, cnidarians show the presence of differentiated cell types in each tissue layer, such as nerve cells, contractile epithelial cells, enzyme-secreting cells, and nutrient-absorbing cells, as well as the presence of intercellular connections. However, the development of organs or organ systems is not advanced in this phylum.

The nervous system is primitive, with nerve cells scattered across the body. This nerve net may show the presence of groups of cells in the form of nerve plexi (singular plexus) or nerve cords. The nerve cells show mixed characteristics of motor as well as sensory neurons. The predominant signaling molecules in these primitive nervous systems are chemical peptides, which perform both excitatory and inhibitory functions. Despite the simplicity of the nervous system, it coordinates the movement of tentacles, the drawing of captured prey to the mouth, the digestion of food, and the expulsion of waste.

The cnidarians perform **extracellular digestion** in which the food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients. The **gastrovascular cavity** has only one opening that serves as both a mouth and an anus, which is termed an incomplete digestive system. Cnidarian cells exchange oxygen and carbon dioxide by diffusion between cells in the epidermis with water in the

environment, and between cells in the gastrodermis with water in the gastrovascular cavity. The lack of a circulatory system to move dissolved gases limits the thickness of the body wall and necessitates a non-living mesoglea between the layers. There is no excretory system or organs, and nitrogenous wastes simply diffuse from the cells into the water outside the animal or in the gastrovascular cavity. There is also no circulatory system, so nutrients must move from the cells that absorb them in the lining of the gastrovascular cavity through the mesoglea to other cells.

The phylum Cnidaria contains about 10,000 described species divided into four classes: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa. The anthozoans, the sea anemones and corals, are all sessile species, whereas the scyphozoans (jellyfish) and cubozoans (box jellies) are swimming forms. The hydrozoans contain sessile forms and swimming colonial forms like the Portuguese Man O' War.

Class Anthozoa

The class Anthozoa includes all cnidarians that exhibit a polyp body plan only; in other words, there is no medusa stage within their life cycle. Examples include sea anemones ([link]), sea pens, and corals, with an estimated number of 6,100 described species. Sea anemones are usually brightly colored and can attain a size of 1.8 to 10 cm in diameter. These animals are usually cylindrical in shape and are attached to a substrate. A mouth opening is surrounded by tentacles bearing cnidocytes.
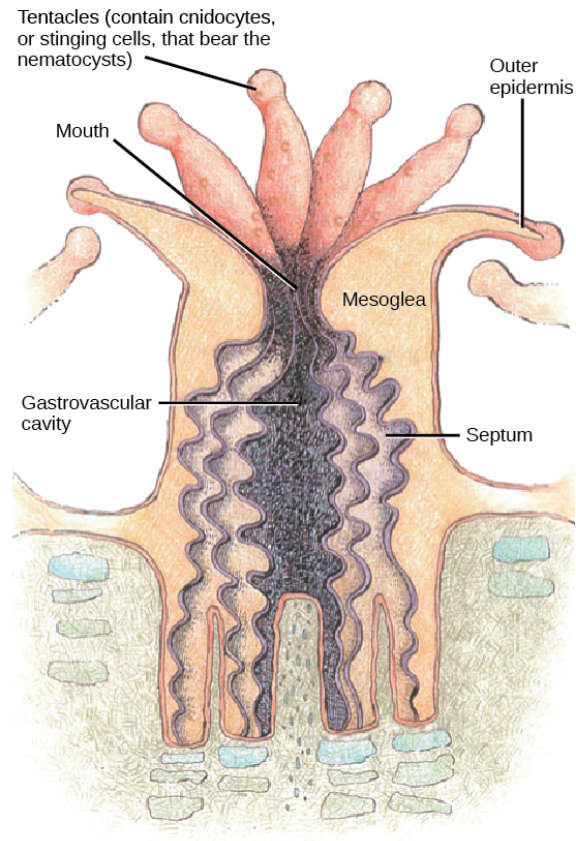
The sea anemone is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Dancing With Ghosts"/Flickr; credit b: modification of work by NOAA)

The mouth of a sea anemone is surrounded by tentacles that bear cnidocytes. The slit-like mouth opening and pharynx are lined by a groove called a **siphonophore**. The pharynx is the muscular part of the digestive system that serves to ingest as well as egest food, and may extend for up to two-thirds the length of the body before opening into the gastrovascular cavity. This cavity is divided into several chambers by longitudinal septa called mesenteries. Each mesentery consists of one ectodermal and one endodermal cell layer with the mesoglea sandwiched in between. Mesenteries do not divide the gastrovascular cavity completely, and the smaller cavities coalesce at the pharyngeal opening. The adaptive benefit of

the mesenteries appears to be an increase in surface area for absorption of nutrients and gas exchange.

Sea anemones feed on small fish and shrimp, usually by immobilizing their prey using the cnidocytes. Some sea anemones establish a mutualistic relationship with hermit crabs by attaching to the crab's shell. In this relationship, the anemone gets food particles from prey caught by the crab, and the crab is protected from the predators by the stinging cells of the anemone. Anemone fish, or clownfish, are able to live in the anemone since they are immune to the toxins contained within the nematocysts.

Anthozoans remain polypoid throughout their lives and can reproduce asexually by budding or fragmentation, or sexually by producing gametes. Both gametes are produced by the polyp, which can fuse to give rise to a free-swimming planula larva. The larva settles on a suitable substratum and develops into a sessile polyp.

Class Scyphozoa

Class Scyphozoa includes all the jellies and is exclusively a marine class of animals with about 200 known species. The defining characteristic of this class is that the medusa is the prominent stage in the life cycle, although there is a polyp stage present. Members of this species range from 2 to 40 cm in length but the largest scyphozoan species, *Cyanea capillata*, can reach a size of 2 m across. Scyphozoans display a characteristic bell-like morphology ([link]).
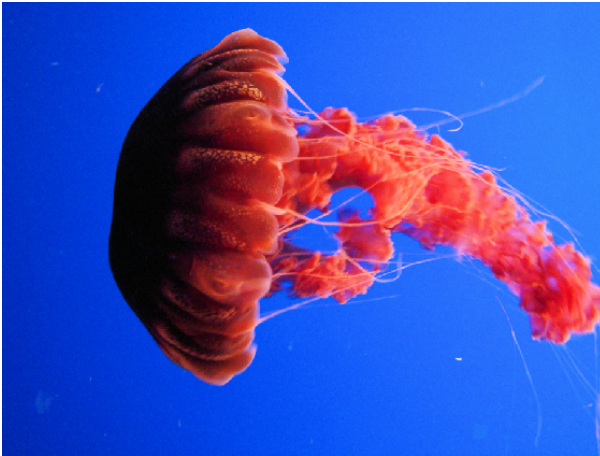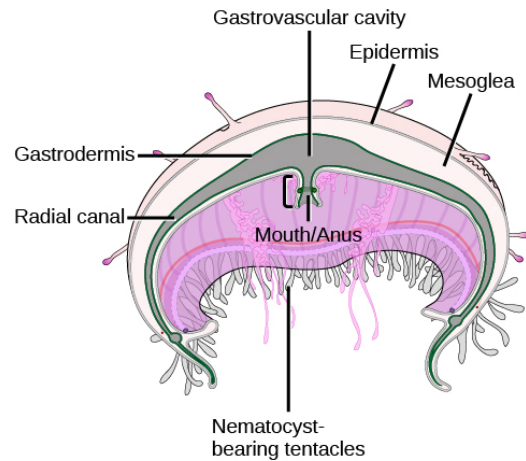
A jelly is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Jimg944"/Flickr; credit b: modification of work by Mariana Ruiz Villareal)

In the jellyfish, a mouth opening is present on the underside of the animal, surrounded by tentacles bearing nematocysts. Scyphozoans live most of their life cycle as free-swimming, solitary carnivores. The mouth leads to the gastrovascular cavity, which may be sectioned into four interconnected sacs, called diverticuli. In some species, the digestive system may be further branched into radial canals. Like the septa in anthozoans, the branched gastrovascular cells serve two functions: to increase the surface area for nutrient absorption and diffusion; thus, more cells are in direct contact with the nutrients in the gastrovascular cavity.

In scyphozoans, nerve cells are scattered all over the body. Neurons may even be present in clusters called rhopalia. These animals possess a ring of muscles lining the dome of the body, which provides the contractile force required to swim through water. Scyphozoans are dioecious animals, that is, the sexes are separate. The gonads are formed from the gastrodermis and gametes are expelled through the mouth. Planula larvae are formed by external fertilization; they settle on a substratum in a polypoid form known as scyphistoma. These forms may produce additional polyps by budding or

may transform into the medusoid form. The life cycle ([link]) of these animals can be described as **polymorphic**, because they exhibit both a medusal and polypoid body plan at some point in their life cycle.
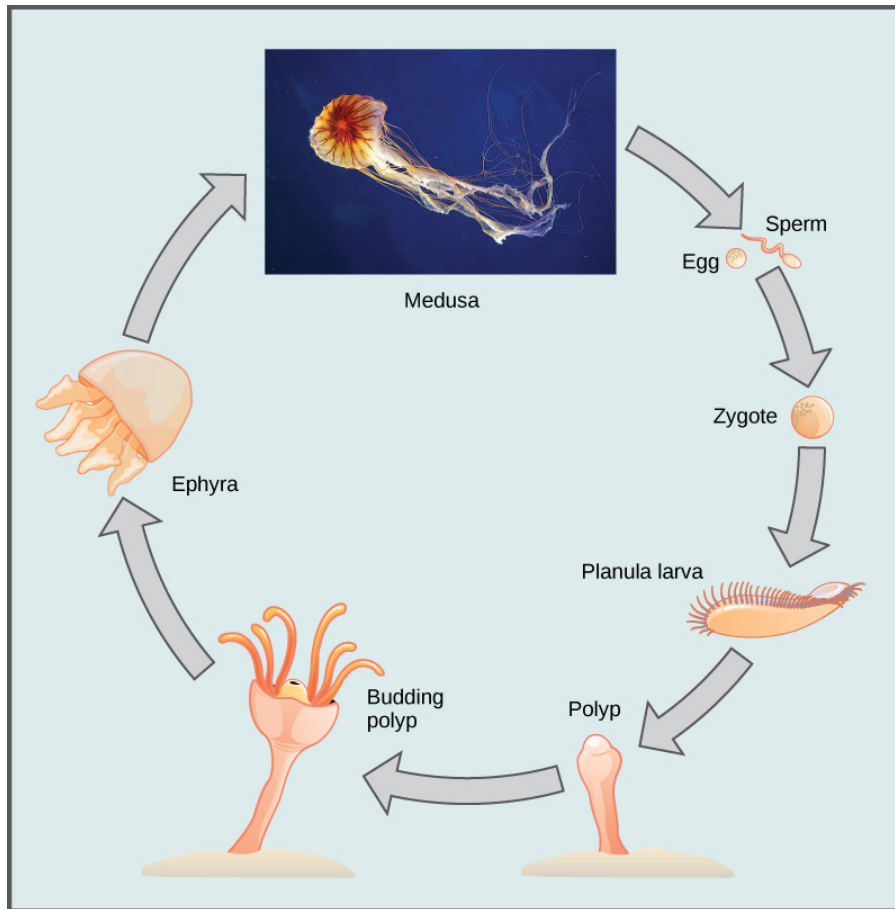
The lifecycle of a jellyfish includes two stages: the medusa stage and the polyp stage. The polyp reproduces asexually by budding, and the medusa reproduces sexually. (credit "medusa": modification of work by Francesco Crippa)

Note:

Class Cubozoa

This class includes jellies that have a box-shaped medusa, or a bell that is square in cross-section; hence, are colloquially known as "box jellyfish." These species may achieve sizes of 15–25 cm. Cubozoans display overall morphological and anatomical characteristics that are similar to those of the scyphozoans. A prominent difference between the two classes is the arrangement of tentacles. This is the most venomous group of all the cnidarians ([link]).

The cubozoans contain muscular pads called pedalia at the corners of the square bell canopy, with one or more tentacles attached to each pedalium. These animals are further classified into orders based on the presence of single or multiple tentacles per pedalium. In some cases, the digestive system may extend into the pedalia. Nematocysts may be arranged in a spiral configuration along the tentacles; this arrangement helps to effectively subdue and capture prey. Cubozoans exist in a polypoid form that develops from a planula larva. These polyps show limited mobility along the substratum and, like scyphozoans, may bud to form more polyps to colonize a habitat. Polyp forms then transform into the medusoid forms.
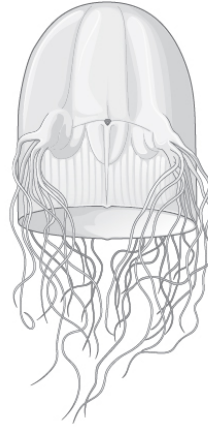
The (a) tiny cubazoan jelly *Malo kingi* is thimble shaped and, like all cubozoan jellies, (b) has four muscular pedalia to which the tentacles attach. *M. kingi* is one of two species of jellies known to cause Irukandji syndrome, a condition characterized by excruciating muscle pain, vomiting, increased heart rate, and psychological symptoms. Two people in Australia, where Irukandji jellies are most commonly found, are believed to have died from Irukandji stings. (c) A sign on a beach in northern Australia warns swimmers of the danger. (credit c: modification of work by Peter Shanks)

Class Hydrozoa

Hydrozoa includes nearly 3,200 species; most are marine, although some freshwater species are known ([link]). Animals in this class are polymorphs, and most exhibit both polypoid and medusoid forms in their lifecycle, although this is variable.

The polyp form in these animals often shows a cylindrical morphology with a central gastrovascular cavity lined by the gastrodermis. The gastrodermis and epidermis have a simple layer of mesoglea sandwiched between them. A mouth opening, surrounded by tentacles, is present at the oral end of the animal. Many hydrozoans form colonies that are composed of a branched colony of specialized polyps that share a gastrovascular cavity, such as in

the colonial hydroid *Obelia*. Colonies may also be free-floating and contain medusoid and polypoid individuals in the colony as in *Physalia* (the Portuguese Man O' War) or *Velella* (By-the-wind sailor). Even other species are solitary polyps (*Hydra*) or solitary medusae (*Gonionemus*). The true characteristic shared by all of these diverse species is that their gonads for sexual reproduction are derived from epidermal tissue, whereas in all other cnidarians they are derived from gastrodermal tissue.

(a) *Obelia*

(b) *Physalia physalis* (Portuguese Man O' War)
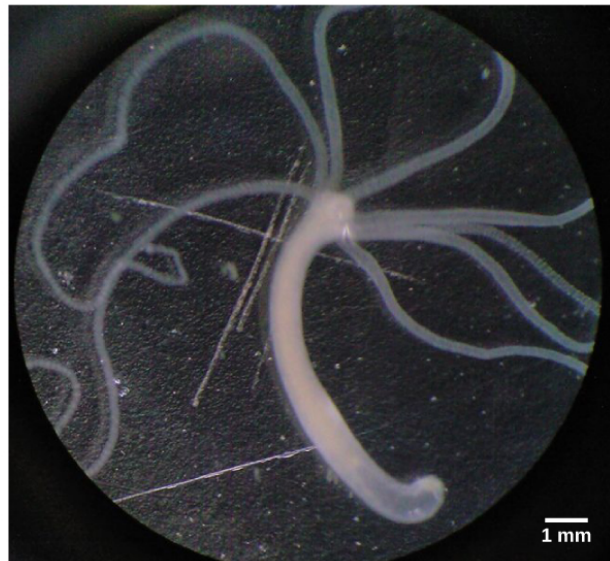
(c) *Velella bae*

(d) *Hydra*

(a) *Obelia*, (b) *Physalia physalis*, known as the Portuguese Man O' War, (c) *Velella bae*, and (d) *Hydra* have different body shapes but all belong to the family Hydrozoa. (credit b: modification of work by NOAA; scale-bar data from Matt Russell)

Section Summary

Cnidarians represent a more complex level of organization than Porifera. They possess outer and inner tissue layers that sandwich a noncellular mesoglea. Cnidarians possess a well-formed digestive system and carry out extracellular digestion. The cnidocyte is a specialized cell for delivering toxins to prey as well as warning off predators. Cnidarians have separate sexes and have a lifecycle that involves morphologically distinct forms. These animals also show two distinct morphological forms—medusoid and polypoid—at various stages in their lifecycle.

Review Questions

Exercise:

Problem: Cnidocytes are found in _____.

   a. phylum Porifera
   b. phylum Nemertea
   c. phylum Nematoda
   d. phylum Cnidaria

Solution:

D

Exercise:

Problem: Cubozoans are _____.

a. polyps
b. medusoids
c. polymorphs
d. sponges

Solution:

C

Free Response

Exercise:

Problem: Explain the function of nematocysts in cnidarians.

Solution:

Nematocysts are "stinging cells" designed to paralyze prey. The nematocysts contain a neurotoxin that renders prey immobile.

Exercise:
Problem:

Compare the structural differences between Porifera and Cnidaria.

Solution:

Poriferans do not possess true tissues, while cnidarians do have tissues. Because of this difference, poriferans do not have a nervous system or muscles for locomotion, which cnidarians have.

Glossary

Cnidaria
    phylum of animals that are diploblastic and have radial symmetry

cnidocyte
    specialized stinging cell found in Cnidaria

epidermis
    outer layer (from ectoderm) that lines the outside of the animal

extracellular digestion
    food is taken into the gastrovascular cavity, enzymes are secreted into
    the cavity, and the cells lining the cavity absorb nutrients

gastrodermis
    inner layer (from endoderm) that lines the digestive cavity

gastrovascular cavity
    opening that serves as both a mouth and an anus, which is termed an
    incomplete digestive system

medusa
    free-floating cnidarian body plan with mouth on underside and
    tentacles hanging down from a bell

mesoglea
    non-living, gel-like matrix present between ectoderm and endoderm in
    cnidarians

nematocyst
    harpoon-like organelle within cnidocyte with pointed projectile and
    poison to stun and entangle prey

polyp
    stalk-like sessile life form of a cnidarians with mouth and tentacles
    facing upward, usually sessile but may be able to glide along surface

polymorphic
    possessing multiple body plans within the lifecycle of a group of
    organisms

siphonophore

tubular structure that serves as an inlet for water into the mantle cavity

Superphylum Lophotrochozoa
By the end of this section, you will be able to:

- Describe the unique anatomical and morphological features of flatworms, rotifers, Nemertea, mollusks, and annelids
- Describe the development of an extracoelomic cavity
- Discuss the advantages of true body segmentation
- Explain the key features of Platyhelminthes and their importance as parasites
- Describe the features of animals classified in phylum Annelida

Animals belonging to superphylum Lophotrochozoa are protostomes, in which the blastopore, or the point of involution of the ectoderm or outer germ layer, becomes the mouth opening to the alimentary canal. This is called protostomy or "first mouth." In protostomy, solid groups of cells split from the endoderm or inner germ layer to form a central mesodermal layer of cells. This layer multiplies into a band and then splits internally to form the coelom; this protostomic coelom is hence termed **schizocoelom**.

As lophotrochozoans, the organisms in this superphylum possess either a lophophore or trochophore larvae. The lophophores include groups that are united by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth. Lophophorata include the flatworms and several other phyla. These clades are upheld when RNA sequences are compared. Trochophore larvae are characterized by two bands of cilia around the body.

The lophotrochozoans are triploblastic and possess an embryonic mesoderm sandwiched between the ectoderm and endoderm found in the diploblastic cnidarians. These phyla are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are symmetrical. It also means the beginning of cephalization, the evolution of a concentration of nervous tissues and sensory organs in the head of the organism, which is where it first encounters its environment.

Phylum Platyhelminthes

The flatworms are acoelomate organisms that include many free-living and parasitic forms. Most of the flatworms are classified in the superphylum Lophotrochozoa, which also includes the mollusks and annelids. The Platyhelminthes consist of two lineages: the Catenulida and the Rhabditophora. The Catenulida, or "chain worms" is a small clade of just over 100 species. These worms typically reproduce asexually by budding. However, the offspring do not fully attach from the parents and, resemble a chain in appearance. All of the remaining flatworms discussed here are part of the Rhabditophora. Many flatworms are parasitic, including important parasites of humans. Flatworms have three embryonic tissue layers that give rise to surfaces that cover tissues (from ectoderm), internal tissues (from mesoderm), and line the digestive system (from endoderm). The epidermal tissue is a single layer cells or a layer of fused cells (syncytium) that covers a layer of circular muscle above a layer of longitudinal muscle. The mesodermal tissues include mesenchymal cells that contain collagen and support secretory cells that secrete mucus and other materials at the surface. The flatworms are acoelomates, so their bodies are solid between the outer surface and the cavity of the digestive system.

Physiological Processes of Flatworms

The free-living species of flatworms are predators or scavengers. Parasitic forms feed on the tissues of their hosts. Most flatworms, such as the planarian shown in [link], have a gastrovascular cavity rather than a complete digestive system. In such animals, the "mouth" is also used to expel waste materials from the digestive system. Some species also have an anal opening. The gut may be a simple sac or highly branched. Digestion is extracellular, with digested materials taken in to the cells of the gut lining by phagocytosis. One group, the cestodes, lacks a digestive system. Flatworms have an excretory system with a network of tubules throughout the body with openings to the environment and nearby flame cells, whose cilia beat to direct waste fluids concentrated in the tubules out of the body. The system is responsible for the regulation of dissolved salts and the excretion of nitrogenous wastes. The nervous system consists of a pair of nerve cords running the length of the body with connections between them and a large ganglion or concentration of nerves at the anterior end of the

worm, where there may also be a concentration of photosensory and chemosensory cells.

There is neither a circulatory nor respiratory system, with gas and nutrient exchange dependent on diffusion and cell-cell junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be "flat" worms.

Most flatworm species are monoecious, and fertilization is typically internal. Asexual reproduction is common in some groups.
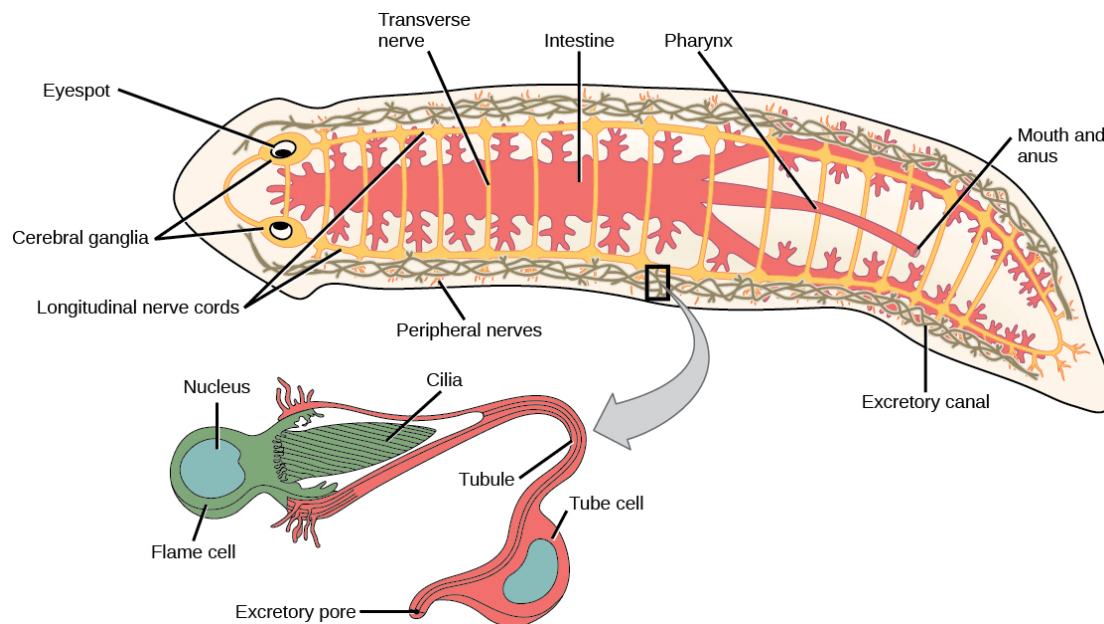
The planarian is a flatworm that has a gastrovascular cavity with one opening that serves as both mouth and anus. The excretory system is made up of tubules connected to excretory pores on both sides of the body. The nervous system is composed of two interconnected nerve cords running the length of the body, with cerebral ganglia and eyespots at the anterior end.

Diversity of Flatworms

Platyhelminthes are traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda ([link]). As discussed above, the relationships among members of these classes is being reassessed, with the turbellarians in particular now viewed as a paraphyletic group, a group that does not have a single common ancestor.

(a) Class Turbellaria
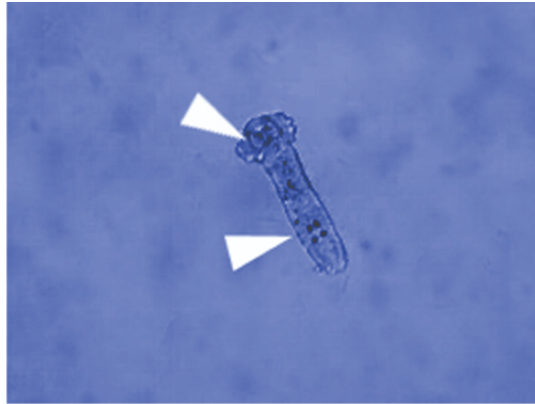
(b) Class Monogenea

(c) Class Trematoda

(d) Class Cestoda

Phylum Platyhelminthes is divided into four classes. (a) Class Turbellaria includes the Bedford's flatworm (*Pseudobiceros bedfordi*), which is about 8–10 cm in length. (b) The parasitic class Monogenea includes *Dactylogyrus* spp. *Dactylogyrus*, commonly called a gill fluke, is about 0.2 mm in length and has

two anchors, indicated by arrows, that it uses to latch onto the gills of host fish. (c) The Trematoda class includes *Fascioloides magna* (right) and *Fasciaola hepatica* (two specimens of left, also known as the common liver fluke). (d) Class Cestoda includes tapeworms such as this *Taenia saginata*. *T. saginata*, which infects both cattle and humans, can reach 4–10 meters in length; the specimen shown here is about 4 meters. (credit a: modification of work by Jan Derk; credit d: modification of work by CDC)

The class Turbellaria includes mainly free-living, marine species, although some species live in freshwater or moist terrestrial environments. The ventral epidermis of turbellarians is ciliated and facilitates their locomotion. Some turbellarians are capable of remarkable feats of regeneration in which they may regrow the body, even from a small fragment.

The monogeneans are ectoparasites, mostly of fish, with simple lifecycles that consist of a free-swimming larva that attaches to a fish to begin transformation to the parasitic adult form. The parasite has only one host and that host is usually only one species. The worms may produce enzymes that digest the host tissues or simply graze on surface mucus and skin particles. Most monogeneans are hermaphroditic, but the male gametes develop first and so cross-fertilization is quite common.

The trematodes, or flukes, are internal parasites of mollusks and many other groups, including humans. Trematodes have complex lifecycles that involve a primary host in which sexual reproduction occurs, and one or more secondary hosts in which asexual reproduction occurs. The primary host is almost always a mollusk. Trematodes are responsible for serious human diseases including schistosomiasis, a blood fluke. The disease infects an estimated 200 million people in the tropics, leading to organ damage and chronic symptoms like fatigue. Infection occurs when the human enters the water and a larva, released from the primary snail host, locates and penetrates the skin. The parasite infects various organs in the body and feeds on red blood cells before reproducing. Many of the eggs are released

in feces and find their way into a waterway, where they are able to reinfect the primary snail host.

The cestodes, or tapeworms, are also internal parasites, mainly of vertebrates ([link]). Tapeworms live in the intestinal tract of the primary host and remain fixed using a sucker on the anterior end, or scolex, of the tapeworm body. The remaining body of the tapeworm is made up of a long series of units called proglottids, each of which may contain an excretory system with flame cells, but contain reproductive structures, both male and female. Tapeworms do not possess a digestive system; instead, they absorb nutrients from the food matter passing them in the host's intestine.

Proglottids are produced at the scolex and gradually migrate to the end of the tapeworm; at this point, they are "mature" and all structures except fertilized eggs have degenerated. Most reproduction occurs by cross-fertilization. The proglottid detaches from the body of the worm and is released into the feces of the organism. The eggs are eaten by an intermediate host. The juvenile worm infects the intermediate host and takes up residence, usually in muscle tissue. When the muscle tissue is eaten by the primary host, the cycle is completed. There are several tapeworm parasites of humans that are transmitted by eating uncooked or poorly cooked pork, beef, and fish.
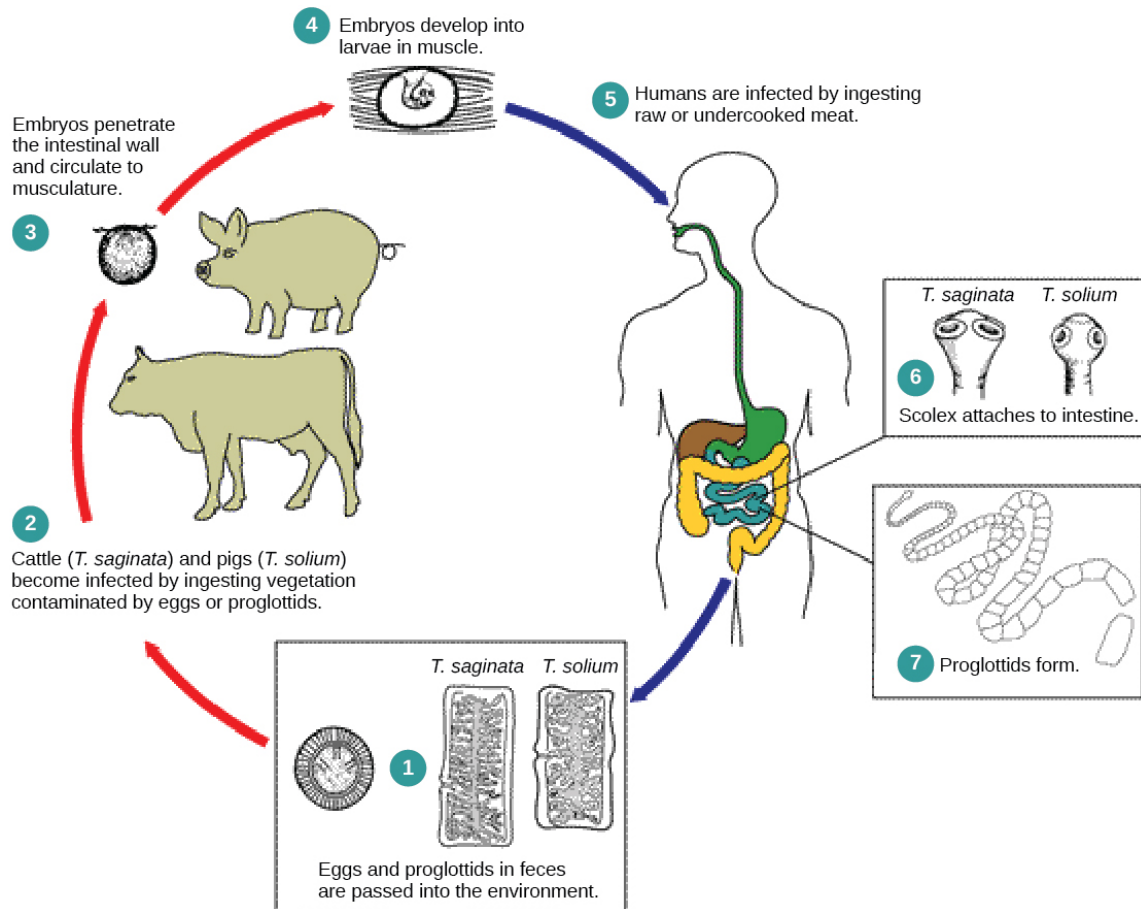
Tapeworm (*Taenia* spp.) infections occur when humans consume raw or undercooked infected meat. (credit: modification of work by CDC)

Phylum Rotifera

The rotifers are a microscopic (about 100 µm to 30 mm) group of mostly aquatic organisms that get their name from the **corona**, a rotating, wheel-like structure that is covered with cilia at their anterior end ([link]). Although their taxonomy is currently in flux, one treatment places the rotifers in three classes: Bdelloidea, Monogononta, and Seisonidea. The classification of the group is currently under revision, however, as more phylogenetic evidence becomes available. It is possible that the "spiny

headed worms" currently in phylum Acanthocephala will be incorporated into this group in the future.

The body form of rotifers consists of a head (which contains the corona), a trunk (which contains the organs), and the foot. Rotifers are typically free-swimming and truly planktonic organisms, but the toes or extensions of the foot can secrete a sticky material forming a holdfast to help them adhere to surfaces. The head contains sensory organs in the form of a bi-lobed brain and small eyespots near the corona.
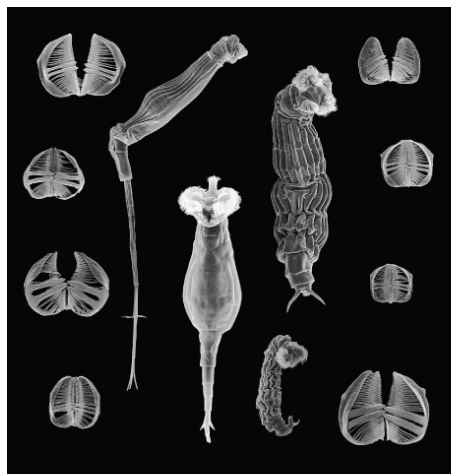
(a) Bdelloidea   (a) Monogonota

Shown are examples from two of the three classes of rotifer. (a) Species from the class Bdelloidea are characterized by a large corona, shown separately from the whole animals in the center of this scanning electron micrograph. (b) *Polyarthra*, from the class Monogononta, has a smaller corona than Bdelloid rotifers, and a single gonad, which give the class its name. (credit a: modification of work by Diego Fontaneto; credit b: modification of work by U.S. EPA; scale-bar data from Cory Zanker)

The rotifers are filter feeders that will eat dead material, algae, and other microscopic living organisms, and are therefore very important components of aquatic food webs. Rotifers obtain food that is directed toward the mouth by the current created from the movement of the corona. The food particles enter the mouth and travel to the **mastax** (pharynx with jaw-like structures). Food then passes by digestive and salivary glands, and into the stomach, then onto the intestines. Digestive and excretory wastes are collected in a cloacal bladder before being released out the anus.

Rotifers are pseudocoelomates commonly found in fresh water and some salt water environments throughout the world. [link] shows the anatomy of a rotifer belonging to class Bdelloidea. About 2,200 species of rotifers have been identified. Rotifers are dioecious organisms (having either male or female genitalia) and exhibit sexual dimorphism (males and females have different forms). Many species are parthenogenic and exhibit haplodiploidy, a method of sex determination in which a fertilized egg develops into a female and an unfertilized egg develops into a male. In many dioecious species, males are short-lived and smaller with no digestive system and a single testis. Females can produce eggs that are capable of dormancy for protection during harsh environmental conditions.
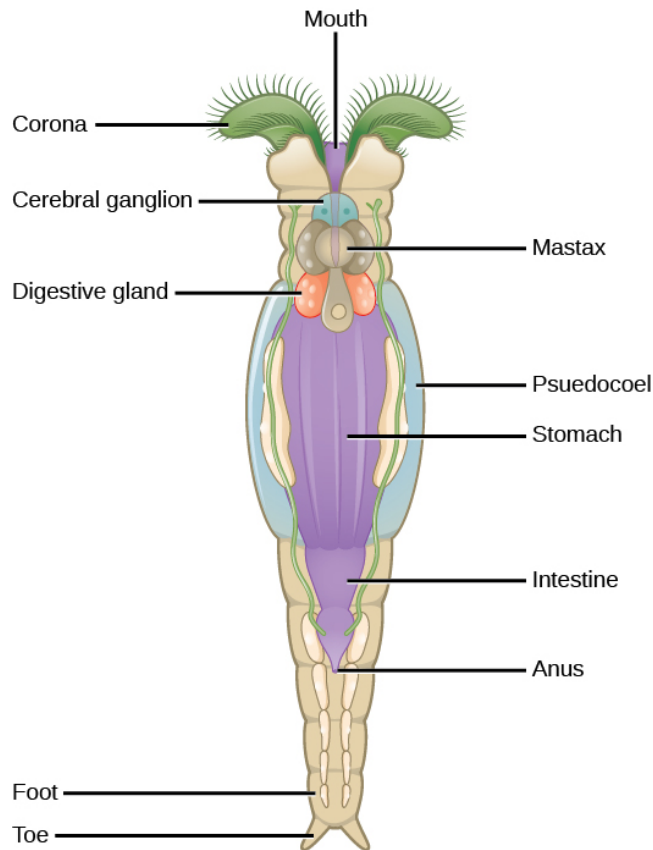
This illustration shows the anatomy of a bdelloid rotifer.

Phylum Nemertea

The Nemertea are colloquially known as ribbon worms. Most species of phylum **Nemertea** are marine, predominantly benthic or bottom dwellers, with an estimated 900 species known. However, nemertini have been recorded in freshwater and terrestrial habitats as well. Most nemerteans are carnivores, feeding on worms, clams, and crustaceans. Some species are scavengers, and some nemertini species, like *Malacobdella grossa*, have also evolved commensalistic relationships with some mollusks. Some species have devastated commercial fishing of clams and crabs. Nemerteans have almost no predators and two species are sold as fish bait.

Morphology

Ribbon worms vary in size from 1 cm to several meters. They show bilateral symmetry and remarkable contractile properties. Because of their contractility, they can change their morphological presentation in response to environmental cues. Animals in phylum Nemertea show a flattened morphology, that is, they are flat from front to back, like a flattened tube. Nemertea are soft and unsegmented animals ([link]).
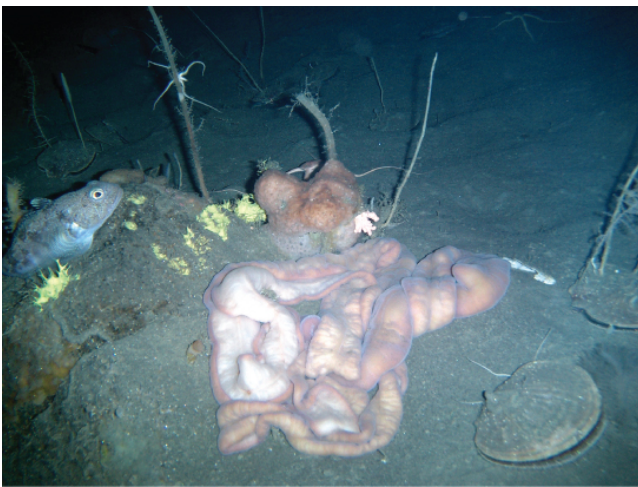
The proboscis worm (*Parborlasia corrugatus*) is a scavenger that combs the sea floor for food. The species is a member of the phylum Nemertea. The specimen shown here was photographed in the Ross Sea, Antarctica. (credit: Henry Kaiser, National Science Foundation)

A unique characteristic of this phylum is the presence of a proboscis enclosed in a **rhynchocoel**. The proboscis serves to capture food and may be ornamented with barbs in some species. The rhynchocoel is a fluid-filled

cavity that extends from the head to nearly two-thirds of the length of the gut in these animals ([link]). The proboscis may be extended or retracted by the retractor muscle attached to the wall of the rhynchocoel.
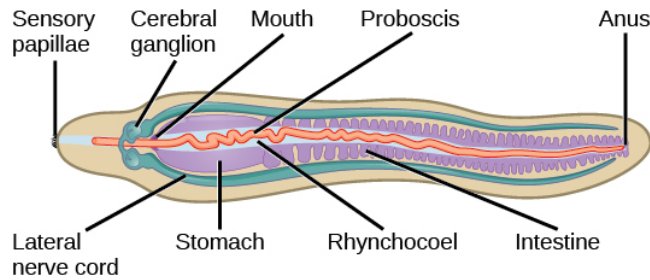
The anatomy of a Nemertean is shown.

Digestive System

The nemertini show a very well-developed digestive system. A mouth opening that is ventral to the rhynchocoel leads into the foregut, followed

by the intestine. The intestine is present in the form of diverticular pouches and ends in a rectum that opens via an anus. Gonads are interspersed with the intestinal diverticular pouches and open outwards via genital pores. A circulatory system consists of a closed loop of a pair of lateral blood vessels. The circulatory system is derived from the coelomic cavity of the embryo. Some animals may also have cross-connecting vessels in addition to lateral ones. Although these are called blood vessels, since they are of coelomic origin, the circulatory fluid is colorless. Some species bear hemoglobin as well as other yellow or green pigments. The blood vessels are connected to the rhynchocoel. The flow of fluid in these vessels is facilitated by the contraction of muscles in the body wall. A pair of protonephridia, or primitive kidneys, is present in these animals to facilitate osmoregulation. Gaseous exchange occurs through the skin in the nemertini.

Nervous System

Nemertini have a ganglion or "brain" situated at the anterior end between the mouth and the foregut, surrounding the digestive system as well as the rhynchocoel. A ring of four nerve masses called "ganglia" composes the brain in these animals. Paired longitudinal nerve cords emerge from the brain ganglia and extend to the posterior end. Ocelli or eyespots are present in pairs, in multiples of two in the anterior portion of the body. It is speculated that the eyespots originate from neural tissue and not from the epidermis.

Reproduction

Animals in phylum Nemertea show sexual dimorphism, although freshwater species may be hermaphroditic. Eggs and sperm are released into the water, and fertilization occurs externally. The zygote then develops into a **planuliform** larva. In some nemertine species, a **pilidium** larva may develop inside the young worm, from a series of imaginal discs. This larval form, characteristically shaped like a deerstalker cap, devours tissues from

the young worm for survival before metamorphosing into the adult-like morphology.

Phylum Mollusca

Phylum **Mollusca** is the predominant phylum in marine environments. It is estimated that 23 percent of all known marine species are mollusks; there are over 75,000 described species, making them the second most diverse phylum of animals. The name "mollusca" signifies a soft body, since the earliest descriptions of mollusks came from observations of unshelled cuttlefish. Mollusks are predominantly a marine group of animals; however, they are known to inhabit freshwater as well as terrestrial habitats. Mollusks display a wide range of morphologies in each class and subclass, but share a few key characteristics, including a muscular foot, a visceral mass containing internal organs, and a mantle that may or may not secrete a shell of calcium carbonate ([link]).

Note:
Art Connection
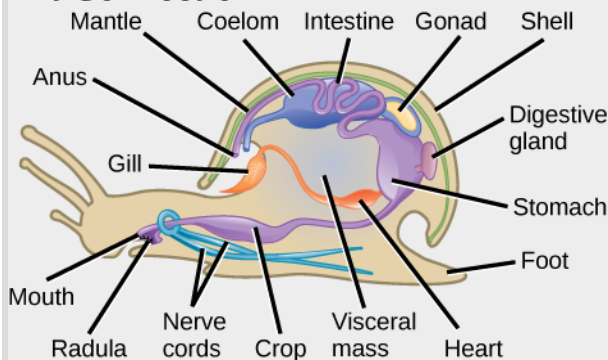
There are many species and variations of mollusks; this illustration shows the anatomy of an aquatic gastropod.

Which of the following statements about the anatomy of a mollusk is false?

a. Mollusks have a radula for grinding food.
b. A digestive gland is connected to the stomach.
c. The tissue beneath the shell is called the mantle.
d. The digestive system includes a gizzard, a stomach, a digestive gland, and the intestine.

Mollusks have a muscular foot, which is used for locomotion and anchorage, and varies in shape and function, depending on the type of mollusk under study. In shelled mollusks, this foot is usually the same size as the opening of the shell. The foot is a retractable as well as an extendable organ. The foot is the ventral-most organ, whereas the mantle is the limiting dorsal organ. Mollusks are eucoelomate, but the coelomic cavity is restricted to a cavity around the heart in adult animals. The mantle cavity develops independently of the coelomic cavity.

The visceral mass is present above the foot, in the visceral hump. This includes digestive, nervous, excretory, reproductive, and respiratory systems. Mollusk species that are exclusively aquatic have gills for respiration, whereas some terrestrial species have lungs for respiration. Additionally, a tongue-like organ called a **radula**, which bears chitinous tooth-like ornamentation, is present in many species, and serves to shred or scrape food. The **mantle** (also known as the pallium) is the dorsal epidermis in mollusks; shelled mollusks are specialized to secrete a chitinous and hard calcareous shell.

Most mollusks are dioecious animals and fertilization occurs externally, although this is not the case in terrestrial mollusks, such as snails and slugs, or in cephalopods. In some mollusks, the zygote hatches and undergoes two larval stages—**trochophore** and **veliger**—before becoming a young adult; bivalves may exhibit a third larval stage, glochidia.

Classification of Phylum Mollusca

Phylum Mollusca is a very diverse (85,000 species) group of mostly marine species. Mollusks have a dramatic variety of form, ranging from large predatory squids and octopus, some of which show a high degree of intelligence, to grazing forms with elaborately sculpted and colored shells. This phylum can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda.

Class Aplacophora ("bearing no plates") includes worm-like animals primarily found in benthic marine habitats. These animals lack a calcareous shell but possess aragonite spicules on their epidermis. They have a rudimentary mantle cavity and lack eyes, tentacles, and nephridia (excretory organs). Members of class Monoplacophora ("bearing one plate") posses a single, cap-like shell that encloses the body. The morphology of the shell and the underlying animal can vary from circular to ovate. A looped digestive system, multiple pairs of excretory organs, many gills, and a pair of gonads are present in these animals. The monoplacophorans were believed extinct and only known via fossil records until the discovery of *Neopilina galathaea* in 1952. Today, scientists have identified nearly two dozen extant species.

Animals in the class Polyplacophora ("bearing many plates") are commonly known as "chitons" and bear an armor-like eight-plated shell ([link]). These animals have a broad, ventral foot that is adapted for suction to rocks and other substrates, and a mantle that extends beyond the shell in the form of a girdle. Calcareous spines may be present on the girdle to offer protection from predators. Respiration is facilitated by **ctenidia** (gills) that are present ventrally. These animals possess a radula that is modified for scraping. The nervous system is rudimentary with only buccal or "cheek" ganglia present at the anterior end. Eyespots are absent in these animals. A single pair of nephridia for excretion is present.

This chiton from the class Polyplacaphora has the eight-plated shell that is indicative of its class. (credit: Jerry Kirkhart)

Class Bivalvia ("two shells") includes clams, oysters, mussels, scallops, and geoducks. Members of this class are found in marine as well as freshwater habitats. As the name suggests, bivalves are enclosed in a pair of shells (valves are commonly called "shells") that are hinged at the dorsal end by shell ligaments as well as shell teeth ([link]). The overall morphology is laterally flattened, and the head region is poorly developed. Eyespots and statocysts may be absent in some species. Since these animals are suspension feeders, a radula is absent in this class of mollusks. Respiration is facilitated by a pair of ctenidia, whereas excretion and osmoregulation are brought about by a pair of nephridia. Bivalves often possess a large mantle cavity. In some species, the posterior edges of the mantle may fuse to form two siphons that serve to take in and exude water.

These mussels, found in the intertidal zone in Cornwall, England, are bivalves. (credit: Mark A. Wilson)

One of the functions of the mantle is to secrete the shell. Some bivalves like oysters and mussels possess the unique ability to secrete and deposit a calcareous **nacre** or "mother of pearl" around foreign particles that may enter the mantle cavity. This property has been commercially exploited to produce pearls.

Note:
Link to Learning

Watch the animations of bivalves feeding: View the process in clams and mussels at these sites.

Animals in class Gastropoda ("stomach foot") include well-known mollusks like snails, slugs, conchs, sea hares, and sea butterflies. Gastropoda includes shell-bearing species as well as species with a reduced shell. These animals are asymmetrical and usually present a coiled shell ([link]). Shells may be **planospiral** (like a garden hose wound up), commonly seen in garden snails, or **conispiral**, (like a spiral staircase), commonly seen in marine conches.

(a)   (b)

(a) Snails and (b) slugs are both gastropods, but slugs lack a shell. (credit a: modification of work by Murray Stevenson; credit b: modification of work by Rosendahl)

The visceral mass in the shelled species displays torsion around the perpendicular axis on the center of the foot, which is the key characteristic of this group, along with a foot that is modified for crawling ([link]). Most gastropods bear a head with tentacles, eyes, and a style. A complex radula is used by the digestive system and aids in the ingestion of food. Eyes may be absent in some gastropods species. The mantle cavity encloses the ctenidia as well as a pair of nephridia.

(a)   (b)
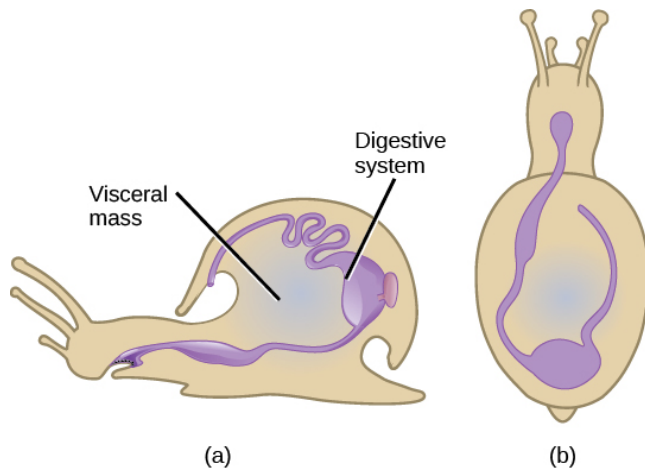
During embryonic development of gastropods, the visceral mass undergoes torsion, or counterclockwise rotation of anatomical features. As a result, the anus of the adult animal is located over the head. Torsion is an independent process from coiling of the shell.

Note:
Everyday Connection
Can Snail Venom Be Used as a Pharmacological Painkiller?
Marine snails of the genus *Conus* ([link]) attack prey with a venomous sting. The toxin released, known as conotoxin, is a peptide with internal disulfide linkages. Conotoxins can bring about paralysis in humans, indicating that this toxin attacks neurological targets. Some conotoxins have been shown to block neuronal ion channels. These findings have led researchers to study conotoxins for possible medical applications. Conotoxins are an exciting area of potential pharmacological development, since these peptides may be possibly modified and used in specific medical conditions to inhibit the activity of specific neurons. For example, these

toxins may be used to induce paralysis in muscles in specific health applications, similar to the use of botulinum toxin. Since the entire spectrum of conotoxins, as well as their mechanisms of action, are not completely known, the study of their potential applications is still in its infancy. Most research to date has focused on their use to treat neurological diseases. They have also shown some efficacy in relieving chronic pain, and the pain associated with conditions like sciatica and shingles. The study and use of biotoxins—toxins derived from living organisms—are an excellent example of the application of biological science to modern medicine.

Members of the genus *Conus* produce neurotoxins that may one day have medical uses. (credit: David Burdick, NOAA)

Class Cephalopoda ("head foot" animals), include octopi, squids, cuttlefish, and nautilus. Cephalopods are a class of shell-bearing animals as well as mollusks with a reduced shell. They display vivid coloration, typically seen in squids and octopi, which is used for camouflage. All animals in this class are carnivorous predators and have beak-like jaws at the anterior end. All cephalopods show the presence of a very well-developed nervous system

along with eyes, as well as a closed circulatory system. The foot is lobed and developed into tentacles, and a funnel, which is used as their mode of locomotion. Suckers are present on the tentacles in octopi and squid. Ctenidia are enclosed in a large mantle cavity and are serviced by large blood vessels, each with its own heart associated with it; the mantle has siphonophores that facilitate exchange of water.

Locomotion in cephalopods is facilitated by ejecting a stream of water for propulsion. This is called "jet" propulsion. A pair of nephridia is present within the mantle cavity. Sexual dimorphism is seen in this class of animals. Members of a species mate, and the female then lays the eggs in a secluded and protected niche. Females of some species care for the eggs for an extended period of time and may end up dying during that time period. Cephalopods such as squids and octopi also produce sepia or a dark ink, which is squirted upon a predator to assist in a quick getaway.

Reproduction in cephalopods is different from other mollusks in that the egg hatches to produce a juvenile adult without undergoing the trochophore and veliger larval stages.

In the shell-bearing *Nautilus* spp., the spiral shell is multi-chambered. These chambers are filled with gas or water to regulate buoyancy. The shell structure in squids and cuttlefish is reduced and is present internally in the form of a squid pen and cuttlefish bone, respectively. Examples are shown in [link].

The (a) nautilus, (b) giant cuttlefish, (c) reef squid, and (d) blue-ring octopus are all members of the class Cephalopoda. (credit a: modification of work by J. Baecker; credit b: modification of work by Adrian Mohedano; credit c: modification of work by Silke Baron; credit d: modification of work by Angell Williams)

Members of class Scaphopoda ("boat feet") are known colloquially as "tusk shells" or "tooth shells," as evident when examining *Dentalium*, one of the few remaining scaphopod genera ([link]). Scaphopods are usually buried in sand with the anterior opening exposed to water. These animals bear a single conical shell, which has both ends open. The head is rudimentary and protrudes out of the posterior end of the shell. These animals do not possess eyes, but they have a radula, as well as a foot modified into tentacles with a bulbous end, known as **captaculae**. Captaculae serve to catch and manipulate prey. Ctenidia are absent in these animals.
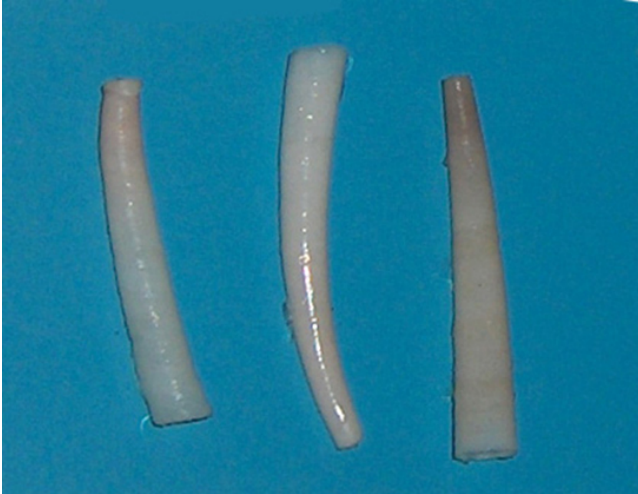
Antalis vulgaris shows the classic Dentaliidae shape that gives these animals their common name of "tusk shell." (credit: Georges Jansoone)

Phylum Annelida

Phylum **Annelida** includes segmented worms. These animals are found in marine, terrestrial, and freshwater habitats, but a presence of water or humidity is a critical factor for their survival, especially in terrestrial habitats. The name of the phylum is derived from the Latin word *annellus*, which means a small ring. Animals in this phylum show parasitic and commensal symbioses with other species in their habitat. Approximately 16,500 species have been described in phylum Annelida. The phylum includes earthworms, polychaete worms, and leeches. Annelids show protostomic development in embryonic stages and are often called "segmented worms" due to their key characteristic of **metamerism**, or true segmentation.

Morphology

Annelids display bilateral symmetry and are worm-like in overall morphology. Annelids have a segmented body plan wherein the internal and external morphological features are repeated in each body segment. Metamerism allows animals to become bigger by adding "compartments" while making their movement more efficient. This metamerism is thought to arise from identical teloblast cells in the embryonic stage, which give rise to identical mesodermal structures. The overall body can be divided into head, body, and pygidium (or tail). The **clitellum** is a reproductive structure that generates mucus that aids in sperm transfer and gives rise to a cocoon within which fertilization occurs; it appears as a fused band in the anterior third of the animal ([link]).

The clitellum, seen here as a protruding segment with different coloration than the rest of the body, is a structure that aids in annelid reproduction. (credit: Rob Hille)

Anatomy

The epidermis is protected by an acellular, external cuticle, but this is much thinner than the cuticle found in the ecdysozoans and does not require periodic shedding for growth. Circular as well as longitudinal muscles are located interior to the epidermis. Chitinous hairlike extensions, anchored in the epidermis and projecting from the cuticle, called **setae/chaetae** are present in every segment. Annelids show the presence of a true coelom, derived from embryonic mesoderm and protostomy. Hence, they are the most advanced worms. A well-developed and complete digestive system is present in earthworms (oligochaetes) with a mouth, muscular pharynx, esophagus, crop, and gizzard being present. The gizzard leads to the intestine and ends in an anal opening. A cross-sectional view of a body segment of an earthworm (a terrestrial type of annelid) is shown in [link]; each segment is limited by a membranous septum that divides the coelomic cavity into a series of compartments.

Annelids possess a closed circulatory system of dorsal and ventral blood vessels that run parallel to the alimentary canal as well as capillaries that service individual tissues. In addition, these vessels are connected by transverse loops in every segment. These animals lack a well-developed respiratory system, and gas exchange occurs across the moist body surface. Excretion is facilitated by a pair of metanephridia (a type of primitive "kidney" that consists of a convoluted tubule and an open, ciliated funnel) that is present in every segment towards the ventral side. Annelids show well-developed nervous systems with a nerve ring of fused ganglia present around the pharynx. The nerve cord is ventral in position and bears enlarged nodes or ganglia in each segment.

Dorsal blood vessel
Intestine
Ventral nerve cord
Ventral blood vessel
Nephridium
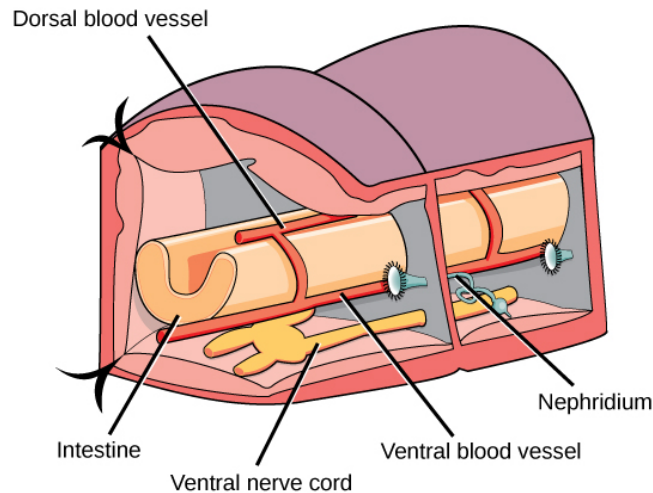
This schematic drawing shows the basic anatomy of annelids in a cross-sectional view.

Annelids may be either monoecious with permanent gonads (as in earthworms and leeches) or dioecious with temporary or seasonal gonads that develop (as in polychaetes). However, cross-fertilization is preferred in hermaphroditic animals. These animals may also show simultaneous hermaphroditism and participate in simultaneous sperm exchange when they are aligned for copulation.

Note:
Link to Learning

This combination video and animation provides a close-up look at annelid anatomy.

Classification of Phylum Annelida

Phylum Annelida contains the class Polychaeta (the polychaetes) and the class Oligochaeta (the earthworms, leeches and their relatives).

Earthworms are the most abundant members of the class Oligochaeta, distinguished by the presence of the clitellum as well as few, reduced chaetae ("oligo- = "few"; -chaetae = "hairs"). The number and size of chaetae are greatly diminished in Oligochaeta compared to the polychaetes (*poly*=many, *chaetae* = hairs). The many chetae of polychaetes are also arranged within fleshy, flat, paired appendages that protrude from each segment called **parapodia**, which may be specialized for different functions in the polychates. The subclass Hirudinea includes leeches such as *Hirudo medicinalis* and *Hemiclepsis marginata*. The class Oligochaeta includes the subclass Hirudinia and the subclass Brachiobdella. A significant difference between leeches and other annelids is the development of suckers at the anterior and posterior ends and a lack of chaetae. Additionally, the segmentation of the body wall may not correspond to the internal segmentation of the coelomic cavity. This adaptation possibly helps the leeches to elongate when they ingest copious quantities of blood from host vertebrates. The subclass Brachiobdella includes species like *Branchiobdella balcanica sketi* and *Branchiobdella astaci*, worms that show similarity with leeches as well as oligochaetes.

(a) (b) (c)

The (a) earthworm, (b) leech, and (c) featherduster are all annelids. (credit a: modification of work by S. Shepherd; credit b: modification of work by "Sarah G..."/Flickr; credit c: modification of work by Chris Gotschalk, NOAA)

Section Summary

Phylum Annelida includes vermiform, segmented animals. Segmentation is seen in internal anatomy as well, which is called metamerism. Annelids are protostomes. These animals have well-developed neuronal and digestive systems. Some species bear a specialized band of segments known as a clitellum. Annelids show the presence numerous chitinous projections termed chaetae, and polychaetes possess parapodia. Suckers are seen in order Hirudinea. Reproductive strategies include sexual dimorphism, hermaphroditism, and serial hermaphroditism. Internal segmentation is absent in class Hirudinea.

Flatworms are acoelomate, triploblastic animals. They lack circulatory and respiratory systems, and have a rudimentary excretory system. This digestive system is incomplete in most species. There are four traditional classes of flatworms, the largely free-living turbellarians, the ectoparasitic monogeneans, and the endoparasitic trematodes and cestodes. Trematodes have complex lifecycles involving a molluscan secondary host and a primary host in which sexual reproduction takes place. Cestodes, or tapeworms, infect the digestive systems of primary vertebrate hosts.

The rotifers are microscopic, multicellular, mostly aquatic organisms that are currently under taxonomic revision. The group is characterized by the rotating, ciliated, wheel-like structure, the corona, on their head. The mastax or jawed pharynx is another structure unique to this group of organisms.

The nemertini are the simplest eucoelomates. These ribbon-shaped animals bear a specialized proboscis enclosed within a rhynchocoel. The development of a closed circulatory system derived from the coelom is a significant difference seen in this species compared to other pseudocoelomate phyla. Alimentary, nervous, and excretory systems are more developed in the nemertini than in less advanced phyla. Embryonic development of nemertine worms proceeds via a planuliform larval stage.

Phylum Mollusca is a large, marine group of invertebrates. Mollusks show a variety of morphological variations within the phylum. This phylum is also distinct in that some members exhibit a calcareous shell as an external means of protection. Some mollusks have evolved a reduced shell. Mollusks are protostomes. The dorsal epidermis in mollusks is modified to form the mantle, which encloses the mantle cavity and visceral organs. This cavity is quite distinct from the coelomic cavity, which in the adult animal surrounds the heart. Respiration is facilitated by gills known as ctenidia. A chitinous-toothed tongue called the radula is present in most mollusks. Early development in some species occurs via two larval stages: trochophore and veliger. Sexual dimorphism is the predominant sexual strategy in this phylum. Mollusks can be divided into seven classes, each with distinct morphological characteristics.

Art Connections

Exercise:

Problem:

[link] Which of the following statements about the anatomy of a mollusk is false?

  a. Mollusks have a radula for grinding food.
  b. A digestive gland is connected to the stomach.
  c. The tissue beneath the shell is called the mantle.
  d. The digestive system includes a gizzard, a stomach, a digestive gland, and the intestine.

Solution:

[link] D

Review Questions

Exercise:

Problem: Annelids have a:

    a. pseudocoelom
    b. a true coelom
    c. no coelom
    d. none of the above

Solution:

B

Exercise:

Problem:

Which group of flatworms are primarily ectoparasites of fish?

    a. monogeneans
    b. trematodes
    c. cestodes
    d. turbellarians

Solution:

A

Exercise:

Problem:A mantle and mantle cavity are present in:

    a. phylum Echinodermata
    b. phylum Adversoidea
    c. phylum Mollusca
    d. phylum Nemertea

Solution:

C

Exercise:

Problem: The rhynchocoel is a _____.

    a. circulatory system
    b. fluid-filled cavity
    c. primitive excretory system
    d. proboscis

Solution:

B

Free Response

Exercise:

Problem: Describe the morphology and anatomy of mollusks.

Solution:

Mollusks have a large muscular foot that may be modified in various ways, such as into tentacles, but it functions in locomotion. They have a mantle, a structure of tissue that covers and encloses the dorsal portion of the animal, and secretes the shell when it is present. The mantle encloses the mantle cavity, which houses the gills (when present), excretory pores, anus, and gonadopores. The coelom of mollusks is restricted to the region around the systemic heart. The main body cavity is a hemocoel. Many mollusks have a radula near the mouth that is used for scraping food.

Exercise:

Problem:

What are the anatomical differences between nemertines and mollusks?

Solution:

Mollusks have a shell, even if it is a reduced shell. Nemertines do not have a shell. Nemertines have a proboscis; mollusks do not. Nemertines have a closed circulatory system, whereas Mollusks have an open circulatory system.

Glossary

Annelida
  phylum of vermiform animals with metamerism

captacula
  tentacle-like projection that is present in tusks shells to catch prey

clitellum
  specialized band of fused segments, which aids in reproduction

conispiral
  shell shape coiled around a horizontal axis

corona
  wheel-like structure on the anterior portion of the rotifer that contains cilia and moves food and water toward the mouth

ctenidium
  specialized gill structure in mollusks

mantle
  (also, pallium) specialized epidermis that encloses all visceral organs and secretes shells

mastax
    jawed pharynx unique to the rotifers

metamerism
    series of body structures that are similar internally and externally, such as segments

Mollusca
    phylum of protostomes with soft bodies and no segmentation

nacre
    calcareous secretion produced by bivalves to line the inner side of shells as well as to coat intruding particulate matter

Nemertea
    phylum of dorsoventrally flattened protostomes known as ribbon worms

parapodium
    fleshy, flat, appendage that protrudes in pairs from each segment of polychaetes

pilidium
    larval form found in some nemertine species

planospiral
    shell shape coiled around a vertical axis

planuliform
    larval form found in phylum Nemertea

radula
    tongue-like organ with chitinous ornamentation

rhynchocoel
    cavity present above the mouth that houses the proboscis

schizocoelom
    coelom formed by groups of cells that split from the endodermal layer

seta/chaeta
        chitinous projection from the cuticle

trochophore
        first of the two larval stages in mollusks

veliger
        second of the two larval stages in mollusks

Superphylum Ecdysozoa
By the end of this section, you will be able to:

- Describe the structural organization of nematodes
- Understand the importance of Caenorhabditis elegans in research
- Compare the internal systems and appendage specializations of phylum Arthropoda
- Discuss the environmental importance of arthropods
- Discuss the reasons for arthropod success and abundance

Superphylum Ecdysozoa

The superphylum Ecdysozoa contains an incredibly large number of species. This is because it contains two of the most diverse animal groups: phylum Nematoda (the roundworms) and Phylum Arthropoda (the arthropods). The most prominant distinguising feature of Ecdysozoans is their tough external covering called the cuticle. The cuticle provides a tough, but flexible exoskeleton tht protects these animals from water loss, predators and other aspects of the external environment. All members of this superphylum periodically molt, or shed their cuticle as they grow. After molting, they secrete a new cuticle that will last until their next growth phase. The process of molting and replacing the cuticle is called ecdysis, which is how the superphylum derived its name.

Phylum Nematoda

The Nematoda, like most other animal phyla, are triploblastic and possess an embryonic mesoderm that is sandwiched between the ectoderm and endoderm. They are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are symmetrical. Furthermore, the nematodes, or roundworms, possess a pseudocoelom and consist of both free-living and parasitic forms.

It has been said that were all the non-nematode matter of the biosphere removed, there would remain a shadow of the former world in the form of nematodes.[footnote] The arthropods, one of the most successful taxonomic groups on the planet, are coelomate organisms characterized by a hard

exoskeleton and jointed appendages. Both the nematodes and arthropods belong to the superphylum Ecdysozoa that is believed to be a clade consisting of all evolutionary descendants from one common ancestor. The name derives from the word ecdysis, which refers to the shedding, or molting, of the exoskeleton. The phyla in this group have a hard cuticle that covers their bodies, which must be periodically shed and replaced for them to increase in size.

Stoll, N. R., "This wormy world. 1947," *Journal of Parasitology* 85(3) (1999): 392-396.

Phylum **Nematoda** includes more than 28,000 species with an estimated 16,000 being parasitic in nature. The name Nematoda is derived from the Greek word "Nemos," which means "thread" and includes roundworms. Nematodes are present in all habitats with a large number of individuals of each species present in each. The free-living nematode, *Caenorhabditis elegans* has been extensively used as a model system in laboratories all over the world.

Morphology

In contrast with cnidarians, nematodes show a tubular morphology and circular cross-section. These animals are pseudocoelomates and show the presence of a complete digestive system with a distinct mouth and anus. This is in contrast with the cnidarians, where only one opening is present (an incomplete digestive system).

The cuticle of Nematodes is rich in collagen and a carbohydrate-protein polymer called chitin, and forms an external "skeleton" outside the epidermis. The cuticle also lines many of the organs internally, including the pharynx and rectum. The epidermis can be either a single layer of cells or a syncytium, which is a multinucleated cell formed from the fusion of uninucleated cells.

The overall morphology of these worms is cylindrical, as seen in [link]. The head is radially symmetrical. A mouth opening is present at the anterior end with three or six lips as well as teeth in some species in the form of cuticle

extensions. Some nematodes may present other external modifications like rings, head shields, or warts. Rings, however, do not reflect true internal body segmentation. The mouth leads to a muscular pharynx and intestine, which leads to a rectum and anal opening at the posterior end. The muscles of nematodes differ from those of most animals: They have a longitudinal layer only, which accounts for the whip-like motion of their movement.

(a)

(b)
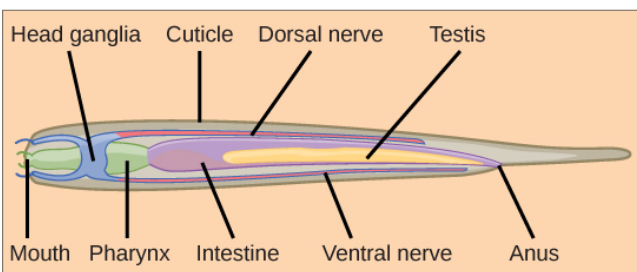
Scanning electron micrograph shows (a) the soybean cyst nematode (*Heterodera glycines*) and a nematode egg. (b) A schematic representation shows the anatomy of a typical nematode. (credit a: modification

of work by USDA ARS; scale-bar
data from Matt Russell)

Excretory System

In nematodes, specialized excretory systems are not well developed. Nitrogenous wastes may be lost by diffusion through the entire body or into the pseudocoelom (body cavity), where they are removed by specialized cells. Regulation of water and salt content of the body is achieved by renette glands, present under the pharynx in marine nematodes.

Nervous system

Most nematodes possess four longitudinal nerve cords that run along the length of the body in dorsal, ventral, and lateral positions. The ventral nerve cord is better developed than the dorsal or lateral cords. All nerve cords fuse at the anterior end, around the pharynx, to form head ganglia or the "brain" of the worm (which take the form of a ring around the pharynx) as well as at the posterior end to form the tail ganglia. In *C. elegans*, the nervous system accounts for nearly one-third of the total number of cells in the animal.

Reproduction

Nematodes employ a variety of reproductive strategies that range from monoecious to dioecious to parthenogenic, depending upon the species under consideration. *C. elegans* is a monoecious species and shows development of ova contained in a uterus as well as sperm contained in the spermatheca. The uterus has an external opening known as the vulva. The female genital pore is near the middle of the body, whereas the male's is at

the tip. Specialized structures at the tail of the male keep him in place while he deposits sperm with copulatory spicules. Fertilization is internal, and embryonic development starts very soon after fertilization. The embryo is released from the vulva during the gastrulation stage. The embryonic development stage lasts for 14 hours; development then continues through four successive larval stages with ecdysis between each stage—L1, L2, L3, and L4—ultimately leading to the development of a young male or female adult worm. Adverse environmental conditions like overcrowding and lack of food can result in the formation of an intermediate larval stage known as the dauer larva.

Note:
Everyday Connection
C. elegans: **The Model System for Linking Developmental Studies with Genetics**
If biologists wanted to research how nicotine dependence develops in the body, how lipids are regulated, or observe the attractant or repellant properties of certain odors, they would clearly need to design three very different experiments. However, they might only need one object of study: *C. elegans*. The nematode *Caenorhabditis elegans* was brought into the focus of mainstream biological research by Dr. Sydney Brenner. Since 1963, Dr. Brenner and scientists worldwide have used this animal as a model system to study various physiological and developmental mechanisms.

C. elegans is a free-living organism found in soil. It is easy to culture this organism on agar plates (10,000 worms/plate), it feeds on *Escherichia coli* (another long-term resident of biological laboratories worldwide), and therefore, it can be readily grown and maintained in a laboratory. The biggest asset of this nematode is its transparency, which helps researchers to observe and monitor changes within the animal with ease. It is also a simple organism with fewer than 1,000 cells and a genome of 20,000 genes. It shows chromosomal organization of DNA into five pairs of autosomes plus a pair of sex chromosomes, making it an ideal candidate to study genetics. Since every cell can be visualized and identified, this organism is useful for studying cellular phenomena like cell-cell

interactions, cell-fate determinations, cell division, apoptosis, and intracellular transport.

Another tremendous asset is the short life cycle of this worm ([link]). It takes only 3 days to achieve the "egg to adult to daughter egg;" therefore, tracking genetic changes is easier in this animal. The total life span of *C. elegans* is 2 to 3 weeks; hence, age-related phenomena are easy to observe. Another feature that makes *C. elegans* an excellent experimental model system is that the position and number of the 959 cells present in adult hermaphrodites of this organism is constant. This feature is extremely significant when studying cell differentiation, cell-cell communication, and apoptosis. Lastly, *C. elegans* is also amenable to genetic manipulations using molecular methods, rounding off its usefulness as a model system. Biologists worldwide have created information banks and groups dedicated to research using *C. elegans*. Their findings have led, for example, to better understandings of cell communication during development, neuronal signaling and insight into lipid regulation (which is important in addressing health issues like the development of obesity and diabetes). In recent years, studies have enlightened the medical community with a better understanding of polycystic kidney disease. This simple organism has led biologists to complex and significant findings, growing the field of science in ways that touch the everyday world.
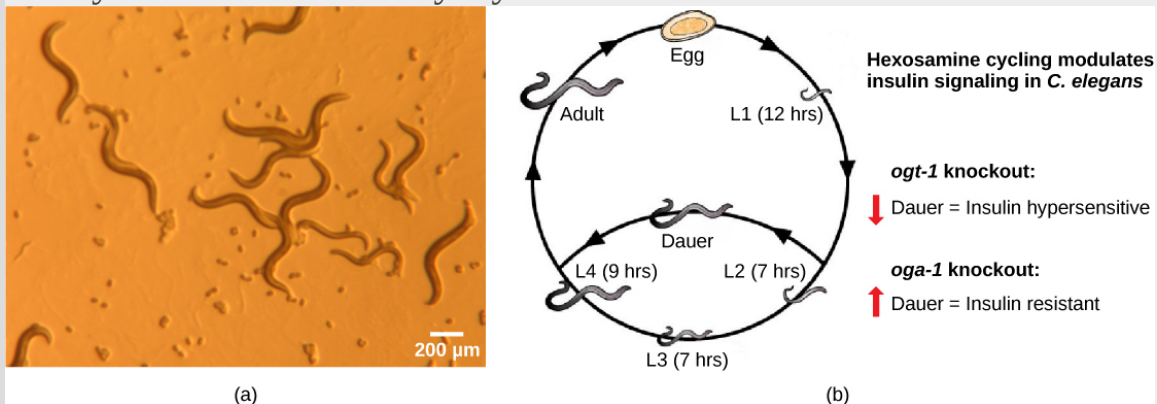
(a) This light micrograph shows *Caenorhabditis elegans*. Its transparent adult stage consists of exactly 959 cells. (b) The life cycle of *C. elegans* has four juvenile stages (L1 through L4) and an adult stage. Under ideal conditions, the nematode spends a set amount of time at each juvenile stage, but under stressful conditions, it may enter a dauer state that does not age. The worm

is hermaphroditic in the adult state, and mating of two worms produces a fertilized egg. (credit a: modification of work by "snickclunk"/Flickr: credit b: modification of work by NIDDK, NIH; scale-bar data from Matt Russell)

A number of common parasitic nematodes serve as prime examples of parasitism. These animals exhibit complex lifecycles that involve multiple hosts, and they can have significant medical and veterinary impacts. Humans may become infected by *Dracunculus medinensis*, known as guinea worms, when they drink unfiltered water containing copepods ([link]). Hookworms, such as *Ancyclostoma* and *Necator*, infest the intestines and feed on the blood of mammals, especially in dogs, cats, and humans. Trichina worms (*Trichinella*) are the causal organism of trichinosis in humans, often resulting from the consumption of undercooked pork; *Trichinella* can infect other mammalian hosts as well. *Ascaris*, a large intestinal roundworm, steals nutrition from its human host and may create physical blockage of the intestines. The filarial worms, such as *Dirofilaria* and *Wuchereria*, are commonly vectored by mosquitoes, which pass the infective agents among mammals through their blood-sucking activity. *Dirofilaria immitis*, a blood-infective parasite, is the notorious dog heartworm species. *Wuchereria bancrofti* infects the lymph nodes of humans, resulting in the non-lethal but deforming condition called elephantiasis, in which parts of the body become swelled to gigantic proportions due to obstruction of lymphatic drainage and inflammation of lymphatic tissues.
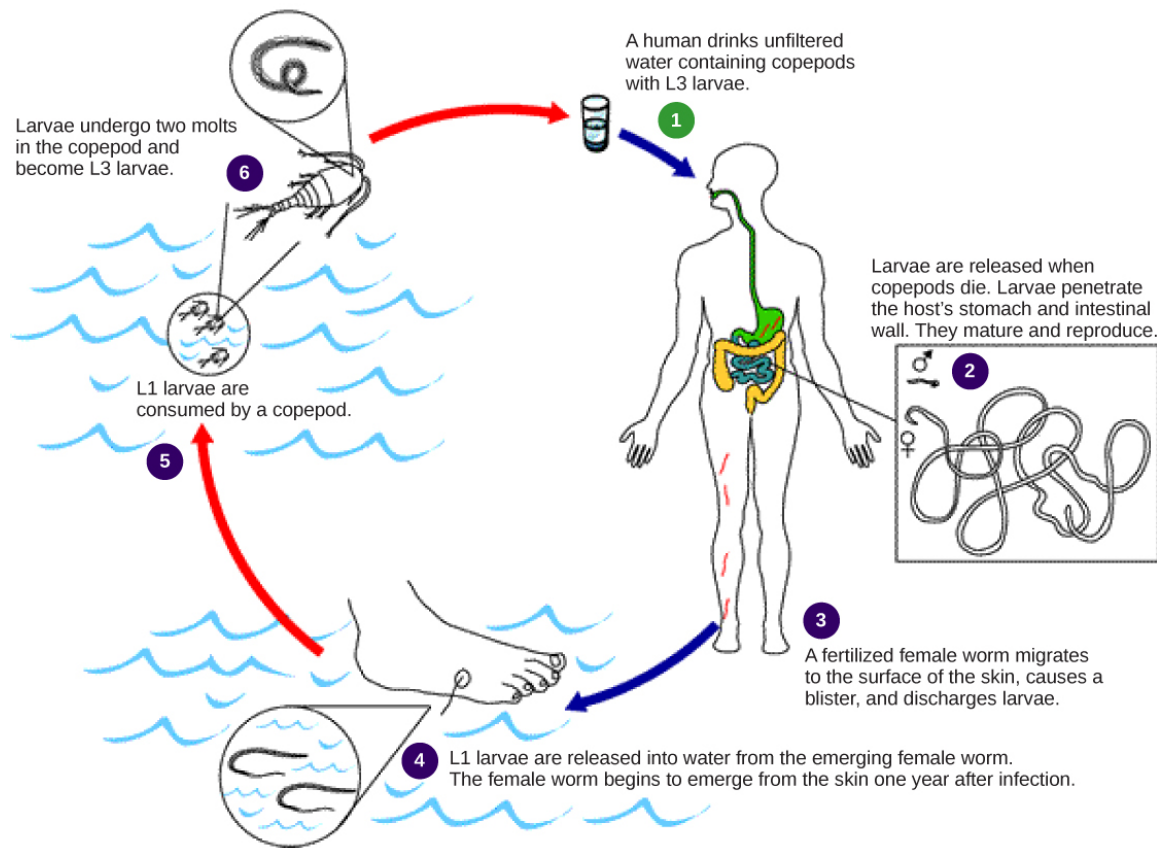
The guinea worm *Dracunculus medinensis* infects about 3.5 million people annually, mostly in Africa. (a) Here, the worm is wrapped around a stick so it can be extracted. (b) Infection occurs when people consume water contaminated by infected copepods, but this can easily be prevented by simple filtration systems. (credit: modification of work by CDC)

Phylum Arthropoda

The name "arthropoda" means "jointed legs" (in the Greek, "arthros" means "joint" and "podos" means "leg"); it aptly describes the enormous number of invertebrates included in this phylum. **Arthropoda** dominate the animal kingdom with an estimated 85 percent of known species included in this phylum and many arthropods yet undocumented. The principal characteristics of all the animals in this phylum are functional segmentation of the body and presence of jointed appendages. Arthropods also show the presence of an exoskeleton made principally of chitin, which is a waterproof, tough polysaccharide. Phylum Arthropoda is the largest phylum in the animal world, and insects form the single largest class within this phylum. Arthropods are eucoelomate, protostomic organisms.

Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. This phylum is further classified into five subphyla: Trilobitomorpha (trilobites, all extinct), Hexapoda (insects and relatives), Myriapoda (millipedes, centipedes, and relatives), Crustaceans (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Chelicerata (horseshoe crabs, arachnids, scorpions, and daddy longlegs). Trilobites are an extinct group of arthropods found chiefly in the pre-Cambrian Era that are probably most closely related to the Chelicerata. These are identified based on fossil records ([link]).

Trilobites, like the one in this

fossil, are an extinct group of arthropods. (credit: Kevin Walsh)

Morphology

A unique feature of animals in the arthropod phylum is the presence of a segmented body and fusion of sets of segments that give rise to functional body regions called tagma. Tagma may be in the form of a head, thorax, and abdomen, or a cephalothorax and abdomen, or a head and trunk. A central cavity, called the **hemocoel** (or blood cavity), is present, and the open circulatory system is regulated by a tubular or single-chambered heart. Respiratory systems vary depending on the group of arthropod: insects and myriapods use a series of tubes (tracheae) that branch through the body, open to the outside through openings called spiracles, and perform gas exchange directly between the cells and air in the tracheae, whereas aquatic crustaceans utilize gills, terrestrial chelicerates employ book lungs, and aquatic chelicerates use book gills ([link]). The book lungs of arachnids (scorpions, spiders, ticks and mites) contain a vertical stack of hemocoel wall tissue that somewhat resembles the pages of a book. Between each of the "pages" of tissue is an air space. This allows both sides of the tissue to be in contact with the air at all times, greatly increasing the efficiency of gas exchange. The gills of crustaceans are filamentous structures that exchange gases with the surrounding water. Groups of arthropods also differ in the organs used for excretion, with crustaceans possessing green glands and insects using Malpighian tubules, which work in conjunction with the hindgut to reabsorb water while ridding the body of nitrogenous waste. The cuticle is the covering of an arthropod. It is made up of two layers: the epicuticle, which is a thin, waxy water-resistant outer layer containing no chitin, and the layer beneath it, the chitinous procuticle. Chitin is a tough, flexible polysaccharide. In order to grow, the arthropod must shed the exoskeleton during a process called ecdysis ("to strip off"); this is a cumbersome method of growth, and during this time, the animal is

vulnerable to predation. The characteristic morphology of representative animals from each subphylum is described below.
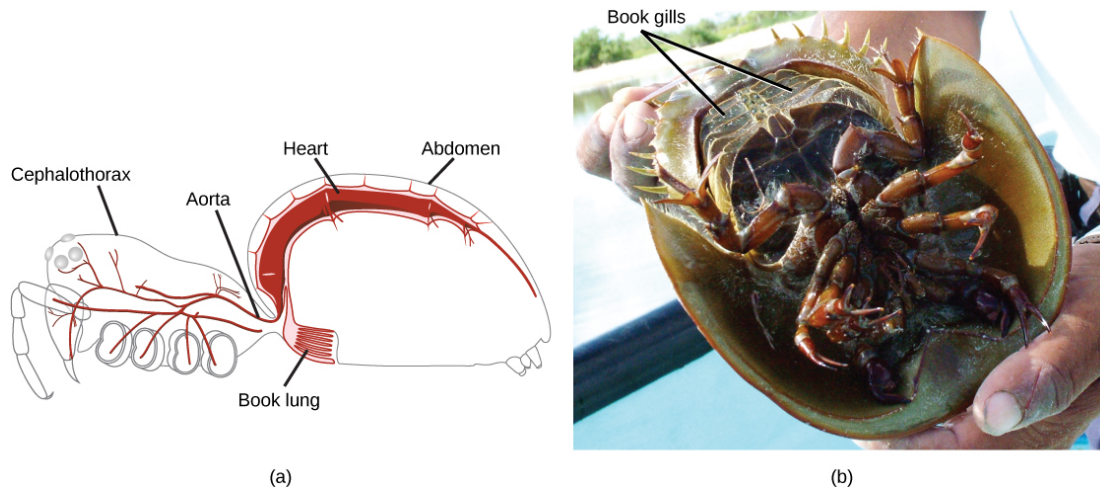
The book lungs of (a) arachnids are made up of alternating air pockets and hemocoel tissue shaped like a stack of books. The book gills of (b) crustaceans are similar to book lungs but are external so that gas exchange can occur with the surrounding water. (credit a: modification of work by Ryan Wilson based on original work by John Henry Comstock; credit b: modification of work by Angel Schatz)

Subphylum Hexapoda

The name Hexapoda denotes the presence of six legs (three pairs) in these animals as differentiated from the number of pairs present in other arthropods. Hexapods are characterized by the presence of a head, thorax, and abdomen, constituting three tagma. The thorax bears the wings as well as six legs in three pairs. Many of the common insects we encounter on a daily basis—including ants, cockroaches, butterflies, and flies—are examples of Hexapoda.

Amongst the hexapods, the insects ([link]) are the largest class in terms of species diversity as well as biomass in terrestrial habitats. Typically, the head bears one pair of sensory antennae, mandibles as mouthparts, a pair of compound eyes, and some ocelli (simple eyes) along with numerous sensory hairs. The thorax bears three pairs of legs (one pair per segment) and two pairs of wings, with one pair each on the second and third thoracic segments. The abdomen usually has eleven segments and bears reproductive apertures. Hexapoda includes insects that are winged (like fruit flies) and wingless (like fleas).

Note:
Art Connection
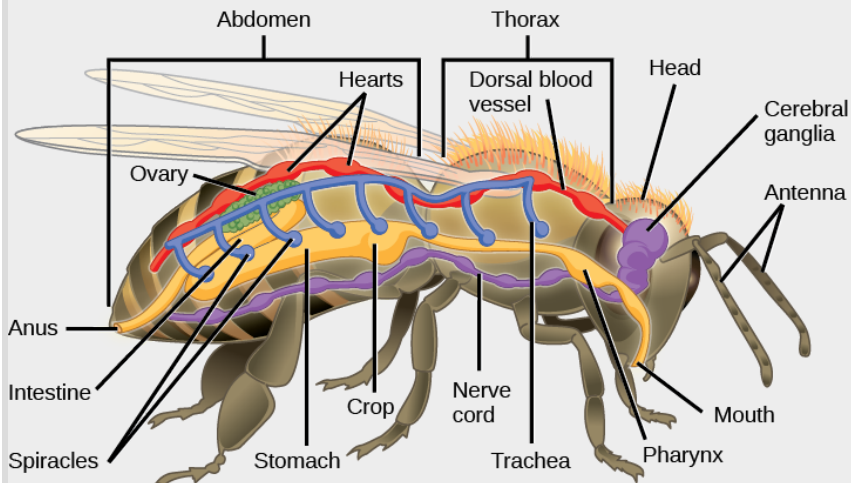
In this basic anatomy of a hexapod insect, note that insects have a developed digestive system (yellow), a respiratory system (blue), a circulatory system (red), and a nervous system (red).

Which of the following statements about insects is false?

a. Insects have both dorsal and ventral blood vessels.
b. Insects have spiracles, openings that allow air to enter.
c. The trachea is part of the digestive system.

d. Insects have a developed digestive system with a mouth, crop, and intestine.

Subphylum Myriapoda

Subphylum Myriapoda includes arthropods with numerous legs. Although the name is hyperbolic in suggesting that myriad legs are present in these invertebrates, the number of legs may vary from 10 to 750. This subphylum includes 13,000 species; the most commonly found examples are millipedes and centipedes. All myriapods are terrestrial animals and prefer a humid environment.

Myriapods are typically found in moist soils, decaying biological material, and leaf litter. Subphylum Myriapoda is divided into four classes: Chilopoda, Symphyla, Diplopoda, and Pauropoda. Centipedes like *Scutigera coleoptrata* ([link]) are classified as chilopods. These animals bear one pair of legs per segment, mandibles as mouthparts, and are somewhat dorsoventrally flattened. The legs in the first segment are modified to form forcipules (poison claws) that deliver poison to prey like spiders and cockroaches, as these animals are all predatory. Millipedes bear two pairs of legs per diplosegment, a feature that results from embryonic fusion of adjacent pairs of body segments, are usually rounder in cross-section, and are herbivores or detritivores. Millipedes have visibly more numbers of legs as compared to centipedes, although they do not bear a thousand legs ([link]).

(a) The *Scutigera coleoptrata* centipede has up to 15 pairs of legs. (b) This North American millipede (*Narceus americanus)* bears many legs, although not a thousand, as its name might suggest. (credit a: modification of work by Bruce Marlin; credit b: modification of work by Cory Zanker)

Subphylum Crustacea

Crustaceans are the most dominant aquatic arthropods, since the total number of marine crustacean species stands at 67,000, but there are also freshwater and terrestrial crustacean species. Krill, shrimp, lobsters, crabs, and crayfish are examples of crustaceans ([link]). Terrestrial species like the wood lice (*Armadillidium* spp.) (also called pill bugs, rolly pollies, potato bugs, or isopods) are also crustaceans, although the number of non-aquatic species in this subphylum is relatively low.

(a)   (b)

The (a) crab and (b) shrimp krill are both crustaceans. (credit a: modification of work by William Warby; credit b: modification of work by Jon Sullivan)

Crustaceans possess two pairs of antennae, mandibles as mouthparts, and **biramous** ("two branched") appendages, which means that their legs are formed in two parts, as distinct from the **uniramous** ("one branched") myriapods and hexapods ([link]).

(a) Biramous appendage (crayfish leg)   (b) Uniramous appendage (insect leg)
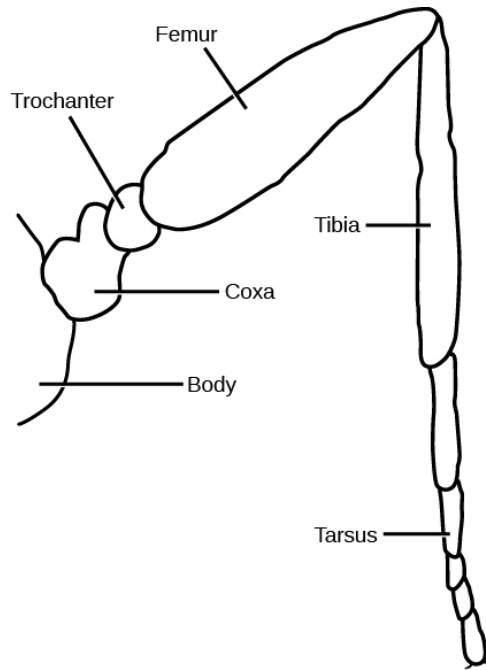
Arthropods may have (a) biramous (two-branched) appendages or (b) uniramous (one-branched) appendages. (credit b: modification of work by Nicholas W. Beeson)

Unlike that of the Hexapoda, the head and thorax of most crustaceans is fused to form a **cephalothorax** ([link]), which is covered by a plate called the carapace, thus producing a body structure of two tagma. Crustaceans have a chitinous exoskeleton that is shed by molting whenever the animal increases in size. The exoskeletons of many species are also infused with calcium carbonate, which makes them even stronger than in other arthropods. Crustaceans have an open circulatory system where blood is

pumped into the hemocoel by the dorsally located heart. Hemocyanin and hemoglobin are the respiratory pigments present in these animals.
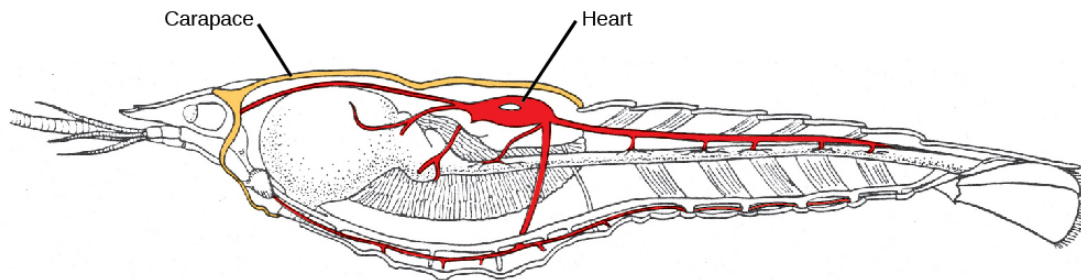
The crayfish is an example of a crustacean. It has a carapace around the cephalothorax and the heart in the dorsal thorax area. (credit: Jane Whitney)

Most crustaceans are dioecious, which means that the sexes are separate. Some species like barnacles may be **hermaphrodites**. Serial hermaphroditism, where the gonad can switch from producing sperm to ova, may also be seen in some species. Fertilized eggs may be held within the female of the species or may be released in the water. Terrestrial crustaceans seek out damp spaces in their habitats to lay eggs.

Larval stages—**nauplius** and **zoea**—are seen in the early development of crustaceans. A **cypris** larva is also seen in the early development of barnacles ([link]).
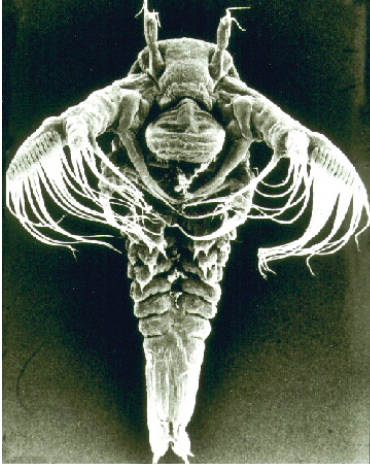
(a) Nauplius larva of a tadpole shrimp   (b) Cypris larva of a barnacle   (c) Zoea larva of a green crab
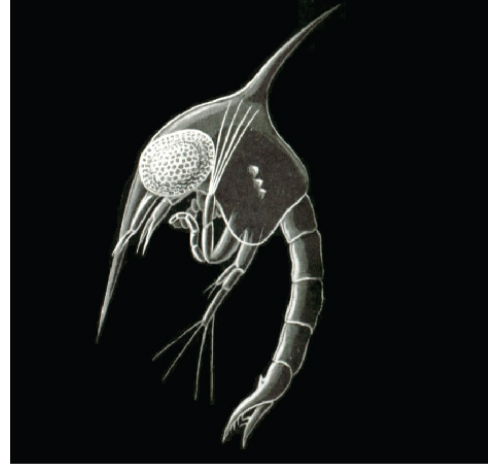
All crustaceans go through different larval stages. Shown are (a) the nauplius larval stage of a tadpole shrimp, (b) the cypris larval stage of a barnacle, and (c) the zoea larval stage of a green crab. (credit a: modification of work by USGS; credit b: modification of work by Mª. C. Mingorance Rodríguez; credit c: modification of work by B. Kimmel based on original work by Ernst Haeckel)

Crustaceans possess a tripartite brain and two compound eyes. Most crustaceans are carnivorous, but herbivorous and detritivorous species are also known. Crustaceans may also be cannibalistic when extremely high populations of these organisms are present.

Subphylum Chelicerata

This subphylum includes animals such as spiders, scorpions, horseshoe crabs, and sea spiders. This subphylum is predominantly terrestrial, although some marine species also exist. An estimated 77,000 species are included in subphylum Chelicerata. Chelicerates are found in almost all habitats.

The body of chelicerates may be divided into two parts: prosoma and opisthosoma, which are basically the equivalents of cephalothorax (usually

smaller) and abdomen (usually larger). A "head" tagmum is not usually discernible. The phylum derives its name from the first pair of appendages: the **chelicerae** ([link]), which are specialized, claw-like or fang-like mouthparts. These animals do not possess antennae. The second pair of appendages is known as **pedipalps**. In some species, like sea spiders, an additional pair of appendages, called **ovigers**, is present between the chelicerae and pedipalps.

The chelicerae (first set of appendages) are well developed in the scorpion. (credit: Kevin Walsh)

Chelicerae are mostly used for feeding, but in spiders, these are often modified into fangs that inject venom into their prey before feeding ([link]). Members of this subphylum have an open circulatory system with a heart that pumps blood into the hemocoel. Aquatic species have gills, whereas terrestrial species have either trachea or book lungs for gaseous exchange.

The trapdoor spider, like all spiders, is a member of the subphylum Chelicerata. (credit: Marshal Hedin)

Most chelicerates ingest food using a preoral cavity formed by the chelicerae and pedipalps. Some chelicerates may secrete digestive enzymes to pre-digest food before ingesting it. Parasitic chelicerates like ticks and mites have evolved blood-sucking apparatuses.

The nervous system in chelicerates consists of a brain and two ventral nerve cords. These animals use external fertilization as well as internal fertilization strategies for reproduction, depending upon the species and its habitat. Parental care for the young ranges from absolutely none to relatively prolonged care.

Note:
Link to Learning

Section Summary

Nematodes are pseudocoelomate animals akin to flatworms, yet display more advanced neuronal development, a complete digestive system, and a body cavity. This phylum includes free-living as well as parasitic organisms like *Caenorhabditis elegans* and *Ascaris* spp., respectively. They include dioeceous as well as hermaphroditic species. Nematodes also possess an excretory system that is not quite well developed. Embryonic development is external and proceeds via three larval stages. A peculiar feature of nematodes is the secretion of a collagenous/chitinous cuticle outside the body.

Arthropods represent the most successful phylum of animal on Earth, in terms of the number of species as well as the number of individuals. These animals are characterized by a segmented body as well as the presence of jointed appendages. In the basic body plan, a pair of appendages is present per body segment. Within the phylum, traditional classification is based on mouthparts, number of appendages, and modifications of appendages present. Arthropods bear a chitinous exoskeleton. Gills, trachea, and book lungs facilitate respiration. Sexual dimorphism is seen in this phylum, and embryonic development includes multiple larval stages.

Art Connections

Exercise:

Problem:

[link] Which of the following statements about insects is false?

- a. Insects have both dorsal and ventral blood vessels.
- b. Insects have spiracles, openings that allow air to enter.
- c. The trachea is part of the digestive system.

d. Insects have a developed digestive system with a mouth, crop, and intestine.

Solution:

C

Review Questions

Exercise:

Problem:

The embryonic development in nematodes can have up to _____ larval stages.

   a. one
   b. two
   c. three
   d. five

Solution:

D

Exercise:

Problem: The nematode cuticle contains _____.

   a. glucose
   b. skin cells
   c. chitin
   d. nerve cells

Solution:

C

Exercise:

Problem: Crustaceans are _____.

    a. ecdysozoans
    b. nematodes
    c. arachnids
    d. parazoans

Solution:

A

Exercise:

Problem: Flies are_____.

    a. chelicerates
    b. hexapods
    c. arachnids
    d. crustaceans

Solution:

B

Free Response

Exercise:

Problem:

Enumerate features of *Caenorhabditis elegans* that make it a valuable model system for biologists.

Solution:

It is a true animal with at least rudiments of the physiological systems —feeding, nervous, muscle, and reproductive—found in "higher animals" like mice and humans. It is so small that large numbers can be raised in Petri dishes. It reproduces rapidly. It is transparent so that every cell in the living animal can be seen under the microscope. Before it dies (after 2–3 weeks), it shows signs of aging and thus may provide general clues as to the aging process.

Exercise:

Problem:

What are the different ways in which nematodes can reproduce?

Solution:

There are nematodes with separate sexes and hermaphrodites in addition to species that reproduce parthenogentically. The nematode *Caenorhabditis elegans* has a self-fertilizing hermaphrodite sex and a pure male sex.

Exercise:

Problem:

Describe the various superclasses that phylum Arthropoda can be divided into.

Solution:

The Arthropoda include the Hexapoda, which are mandibulates with six legs, the Myriapoda, which are mandibulates with many legs and include the centipedes and millipedes, the Crustacea, which are mostly marine mandibulates, and the Chelicerata, which include the spiders and scorpions and their kin.

Exercise:

Problem:

Compare and contrast the segmentation seen in phylum Annelida with that seen in phylum Arthropoda.

Solution:

Arthropods have an exoskeleton, which is missing in annelids. Arthropod segmentation is more specialized with major organs concentrated in body tagma. Annelid segmentation is usually more uniform with the intestine extending through most segments.

Glossary

Arthropoda
> phylum of animals with jointed appendages

biramous
> referring to two branches per appendage

cephalothorax
> fused head and thorax in some species

chelicera
> modified first pair of appendages in subphylum Chelicerata

cuticle (animal)
> the tough, external layer possessed by members of the invertebrate class Ecdysozoa that is periodically molted and replaced

cypris
> larval stage in the early development of crustaceans

hemocoel
> internal body cavity seen in arthropods

hermaphrodite

referring to an animal where both male and female gonads are present in the same individual

nauplius
   larval stage in the early development of crustaceans

Nematoda
   phylum of worm-like animals that are triploblastic, pseudocoelomates that can be free-living or parasitic

oviger
   additional pair of appendages present on some arthropods between the chelicerae and pedipalps

pedipalp
   second pair of appendages in Chelicerata

uniramous
   referring to one branch per appendage

zoea
   larval stage in the early development of crustaceans

Superphylum Deuterostomia
By the end of this section, you will be able to:

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates

The phyla Echinodermata and Chordata (the phylum in which humans are placed) both belong to the superphylum Deuterostomia. Recall that protostome and deuterostomes differ in certain aspects of their embryonic development, and they are named based on which opening of the digestive cavity develops first. The word deuterostome comes from the Greek word meaning "mouth second," indicating that the anus is the first to develop. There are a series of other developmental characteristics that differ between protostomes and deuterostomes, including the mode of formation of the coelom and the early cell division of the embryo. In deuterostomes, internal pockets of the endodermal lining called the **archenteron** fuse to form the coelom. The endodermal lining of the archenteron (or the primitive gut) forms membrane protrusions that bud off and become the mesodermal layer. These buds, known as coelomic pouches, fuse to form the coelomic cavity, as they eventually separate from the endodermal layer. The resultant coelom is termed an **enterocoelom**. The archenteron develops into the alimentary canal, and a mouth opening is formed by invagination of ectoderm at the pole opposite the blastopore of the gastrula. The blastopore forms the anus of the alimentary system in the juvenile and adult forms. The fates of embryonic cells in deuterostomes can be altered if they are experimentally moved to a different location in the embryo due to indeterminant cleavage in early embryogenesis.

Phylum Echinodermata

Echinodermata are so named owing to their spiny skin (from the Greek "echinos" meaning "spiny" and "dermos" meaning "skin"), and this phylum is a collection of about 7,000 described living species. **Echinodermata** are exclusively marine organisms. Sea stars ([link]), sea cucumbers, sea urchins, sand dollars, and brittle stars are all examples of echinoderms. To date, no freshwater or terrestrial echinoderms are known.

Morphology and Anatomy

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles, although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells and may possess pigment cells, giving vivid colors to these animals, as well as cells laden with toxins. Gonads are present in each arm. In echinoderms like sea stars, every arm bears two rows of tube feet on the oral side. These tube feet help in attachment to the substratum. These animals possess a true coelom that is modified into a unique circulatory system called a **water vascular system**. An interesting feature of these animals is their power to regenerate, even when over 75 percent of their body mass is lost.
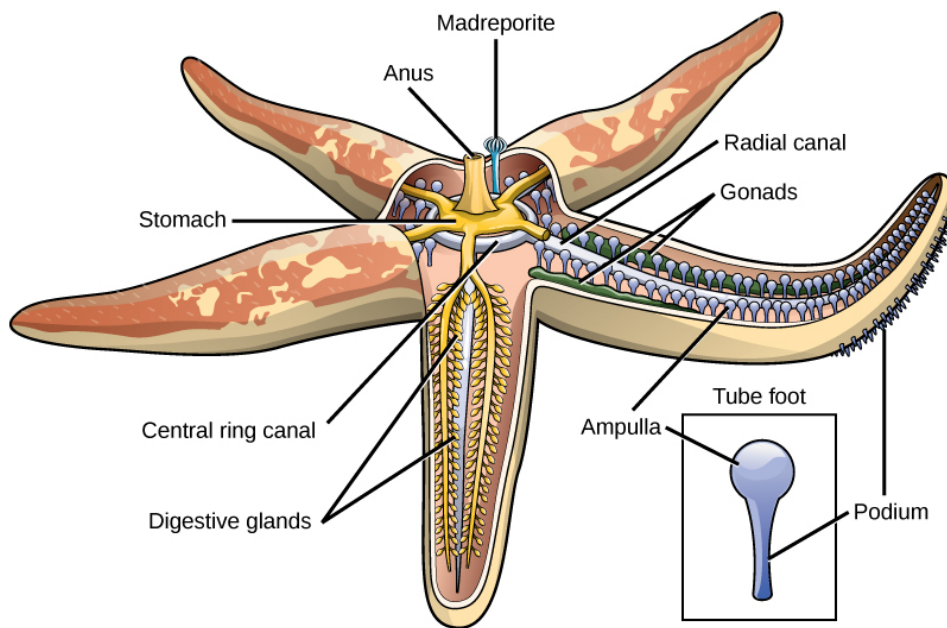
This diagram shows the anatomy of a sea star.

Water Vascular System

Echinoderms possess a unique ambulacral or water vascular system, consisting of a central ring canal and radial canals that extend along each arm. Water circulates through these structures and facilitates gaseous exchange as well as nutrition, predation, and locomotion. The water vascular system also projects from holes in the skeleton in the form of tube feet. These tube feet can expand or contract based on the volume of water present in the system of that arm. By using hydrostatic pressure, the animal can either protrude or retract the tube feet. Water enters the madreporite on the aboral side of the echinoderm. From there, it passes into the stone canal, which moves water into the ring canal. The ring canal connects the radial canals (there are five in a pentaradial animal), and the radial canals move water into the ampullae, which have tube feet through which the water moves. By moving water through the unique water vascular system, the echinoderm can move and force open mollusk shells during feeding.

Nervous System

The nervous system in these animals is a relatively simple structure with a nerve ring at the center and five radial nerves extending outward along the arms. Structures analogous to a brain or derived from fusion of ganglia are not present in these animals.

Excretory System

Podocytes, cells specialized for ultrafiltration of bodily fluids, are present near the center of echinoderms. These podocytes are connected by an internal system of canals to an opening called the **madreporite**.

Reproduction

Echinoderms are sexually dimorphic and release their eggs and sperm cells into water; fertilization is external. In some species, the larvae divide

asexually and multiply before they reach sexual maturity. Echinoderms may also reproduce asexually, as well as regenerate body parts lost in trauma.

Classes of Echinoderms

This phylum is divided into five extant classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies or feather stars), and Holothuroidea (sea cucumbers) ([link]).

The most well-known echinoderms are members of class Asteroidea, or sea stars. They come in a large variety of shapes, colors, and sizes, with more than 1,800 species known so far. The key characteristic of sea stars that distinguishes them from other echinoderm classes includes thick arms (ambulacra) that extend from a central disk where organs penetrate into the arms. Sea stars use their tube feet not only for gripping surfaces but also for grasping prey. Sea stars have two stomachs, one of which can protrude through their mouths and secrete digestive juices into or onto prey, even before ingestion. This process can essentially liquefy the prey and make digestion easier.

Note:
Link to Learning

Explore the sea star's body plan up close, watch one move across the sea floor, and see it devour a mussel.

Brittle stars belong to the class Ophiuroidea. Unlike sea stars, which have plump arms, brittle stars have long, thin arms that are sharply demarcated from the central disk. Brittle stars move by lashing out their arms or wrapping them around objects and pulling themselves forward. Sea urchins and sand dollars are examples of Echinoidea. These echinoderms do not have arms, but are hemispherical or flattened with five rows of tube feet that help them in slow movement; tube feet are extruded through pores of a continuous internal shell called a test. Sea lilies and feather stars are examples of Crinoidea. Both of these species are suspension feeders. Sea cucumbers of class Holothuroidea are extended in the oral-aboral axis and have five rows of tube feet. These are the only echinoderms that demonstrate "functional" bilateral symmetry as adults, because the uniquely extended oral-aboral axis compels the animal to lie horizontally rather than stand vertically.
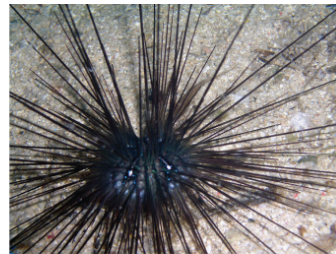
(a) (b) (c)

(d) (e)

Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (e) sea cucumbers, representing class Holothuroidea. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua

Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed Bierman)

Phylum Chordata

Animals in the phylum **Chordata** share four key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. In some groups, some of these traits are present only during embryonic development. In addition to containing vertebrate classes, the phylum Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets). Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

Section Summary

Echinoderms are deuterostomic marine organisms. This phylum of animals bears a calcareous endoskeleton composed of ossicles. These animals also have spiny skin. Echinoderms possess water-based circulatory systems. A pore termed the madreporite is the point of entry and exit for water into the water vascular system. Osmoregulation is carried out by specialized cells known as podocytes.

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

Review Questions

Exercise:

Problem: Echinoderms have _____.

    a. triangular symmetry
    b. radial symmetry
    c. hexagonal symmetry
    d. pentaradial symmetry

Solution:

D

Exercise:

Problem: The circulatory fluid in echinoderms is _____.

    a. blood
    b. mesohyl
    c. water
    d. saline

Solution:

C

Free Response

Exercise:

Problem:

Describe the different classes of echinoderms using examples.

Solution:

The Asteroidea are the sea stars, the Echinoidea are the sea urchins and sand dollars, the Ophiuroidea are the brittle stars, the Crinoidea are the sea lilies and feather stars, the Holothuroidea are the sea cucumbers.

Glossary

archenteron
    primitive gut cavity within the gastrula that opens outwards via the blastopore

Chordata
    phylum of animals distinguished by their possession of a notochord, a dorsal, hollow nerve cord, pharyngeal slits, and a post-anal tail at some point in their development

Echinodermata
    phylum of deuterostomes with spiny skin; exclusively marine organisms

enterocoelom
    coelom formed by fusion of coelomic pouches budded from the endodermal lining of the archenteron

madreporite
    pore for regulating entry and exit of water into the water vascular system

water vascular system
    system in echinoderms where water is the circulatory fluid

Introduction
class="introduction"

Examples of critically endangered vertebrate species include (a) the Siberian tiger (*Panthera tigris*), (b) the mountain gorilla (*Gorilla beringei*), and (c) the Philippine eagle (*Pithecophega jefferyi*). (credit a: modification of work by Dave Pape; credit b: modification of work by Dave Proffer; credit c: modification of work by "cuatrok77"/Flickr)

(a)   (b)   (c)

Vertebrates are among the most recognizable organisms of the animal kingdom. More than 62,000 vertebrate species have been identified. The vertebrate species now living represent only a small portion of the vertebrates that have existed. The best-known extinct vertebrates are the dinosaurs, a unique group of reptiles, which reached sizes not seen before or after in terrestrial animals. They were the dominant terrestrial animals for 150 million years, until they died out in a mass extinction near the end of the Cretaceous period. Although it is not known with certainty what caused their extinction, a great deal is known about the anatomy of the dinosaurs, given the preservation of skeletal elements in the fossil record.

Currently, a number of vertebrate species face extinction primarily due to habitat loss and pollution. According to the International Union for the Conservation of Nature, more than 6,000 vertebrate species are classified as threatened. Amphibians and mammals are the classes with the greatest percentage of threatened species, with 29 percent of all amphibians and 21 percent of all mammals classified as threatened. Attempts are being made around the world to prevent the extinction of threatened species. For example, the Biodiversity Action Plan is an international program, ratified by 188 countries, which is designed to protect species and habitats.

Chordates
By the end of this section, you will be able to:

- Describe the distinguishing characteristics of chordates
- Identify the derived character of craniates that sets them apart from other chordates
- Describe the developmental fate of the notochord in vertebrates

Vertebrates are members of the kingdom Animalia and the phylum Chordata ([link]). Recall that animals that possess bilateral symmetry can be divided into two groups—protostomes and deuterostomes—based on their patterns of embryonic development. The deuterostomes, whose name translates as "second mouth," consist of two phyla: Chordata and Echinodermata. Echinoderms are invertebrate marine animals that have pentaradial symmetry and a spiny body covering, a group that includes sea stars, sea urchins, and sea cucumbers. The most conspicuous and familiar members of Chordata are vertebrates, but this phylum also includes two groups of invertebrate chordates.
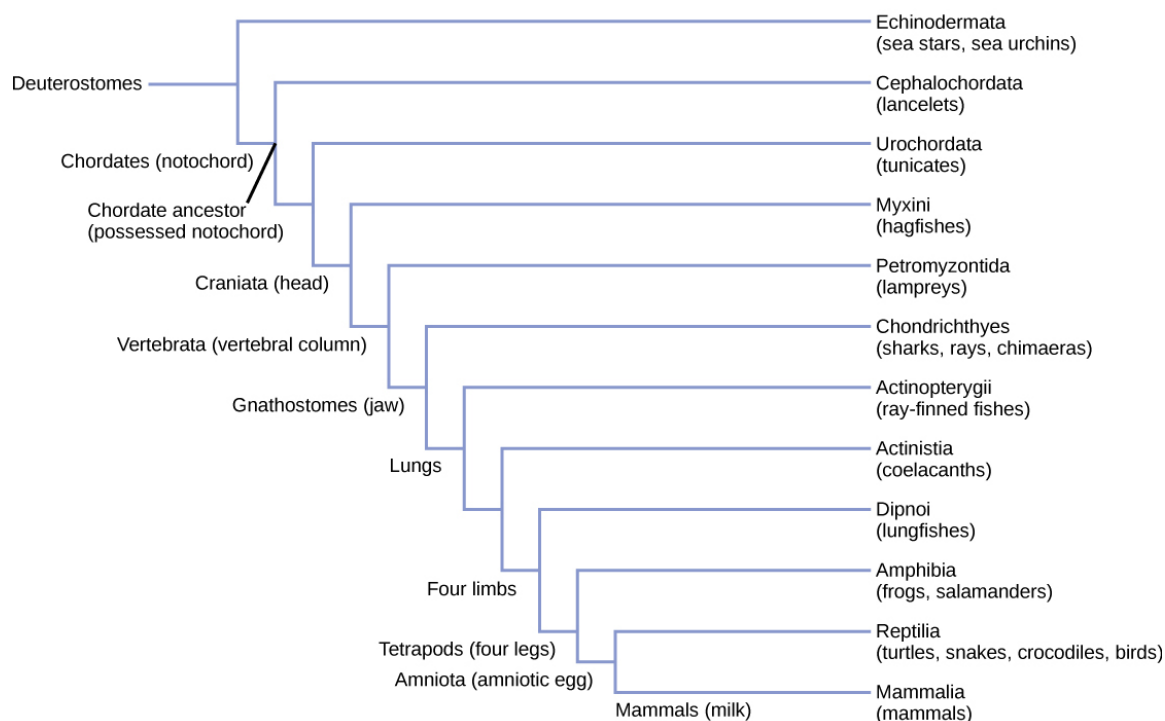
All chordates are deuterostomes possessing a notochord.

Characteristics of Chordata

Animals in the phylum **Chordata** share four key features that appear at some stage during their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail ([link]). In some groups, some of these are present only during embryonic development.

The chordates are named for the **notochord**, which is a flexible, rod-shaped structure that is found in the embryonic stage of all chordates and in the adult stage of some chordate species. It is located between the digestive tube and the nerve cord, and provides skeletal support through the length of the body. In some chordates, the notochord acts as the primary axial support of the body throughout the animal's lifetime. In vertebrates, the notochord is present during embryonic development, at which time it induces the development of the neural tube and serves as a support for the developing embryonic body. The notochord, however, is not found in the postnatal stage of vertebrates; at this point, it has been replaced by the vertebral column (that is, the spine).

Note:
Art Connection
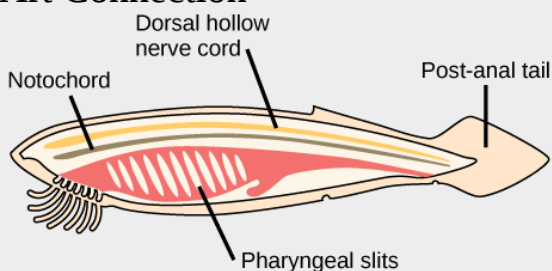
In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

Which of the following statements about common features of chordates is true?

a. The dorsal hollow nerve cord is part of the chordate central nervous system.
b. In vertebrate fishes, the pharyngeal slits become the gills.
c. Humans are not chordates because humans do not have a tail.
d. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

The **dorsal hollow nerve cord** derives from ectoderm that rolls into a hollow tube during development. In chordates, it is located dorsal to the notochord. In contrast, other animal phyla are characterized by solid nerve cords that are located either ventrally or laterally. The nerve cord found in most chordate embryos develops into the brain and spinal cord, which compose the central nervous system.

Pharyngeal slits are openings in the pharynx (the region just posterior to the mouth) that extend to the outside environment. In organisms that live in aquatic environments, pharyngeal slits allow for the exit of water that enters the mouth during feeding. Some invertebrate chordates use the pharyngeal slits to filter food out of the water that enters the mouth. In vertebrate fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, into jaw supports. In tetrapods, the slits are modified into components of the ear and tonsils. **Tetrapod** literally means "four-footed," which refers to the phylogenetic history of various groups that evolved accordingly, even though some now possess fewer than two pairs of walking appendages. Tetrapods include amphibians, reptiles, birds, and mammals.

The **post-anal tail** is a posterior elongation of the body, extending beyond the anus. The tail contains skeletal elements and muscles, which provide a source of locomotion in aquatic species, such as fishes. In some terrestrial

vertebrates, the tail also helps with balance, courting, and signaling when danger is near. In humans, the post-anal tail is vestigial, that is, reduced in size and nonfunctional.

Chordates and the Evolution of Vertebrates

Chordata also contains two clades of invertebrates: Urochordata and Cephalochordata. Members of these groups also possess the four distinctive features of chordates at some point during their development.

Urochordata

Members of **Urochordata** are also known as **tunicates** ([link]). The name tunicate derives from the cellulose-like carbohydrate material, called the tunic, which covers the outer body of tunicates. Although adult tunicates are classified as chordates, they do not have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits. The larval form, however, possesses all four structures. Most tunicates are hermaphrodites. Tunicate larvae hatch from eggs inside the adult tunicate's

body. After hatching, a tunicate larva swims for a few days until it finds a suitable surface on which it can attach, usually in a dark or shaded location. It then attaches via the head to the surface and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear.
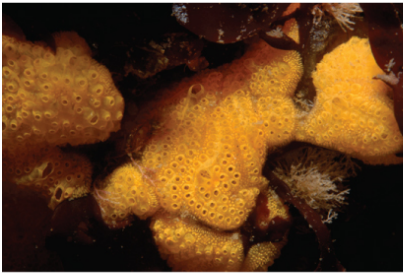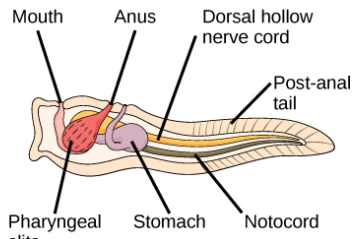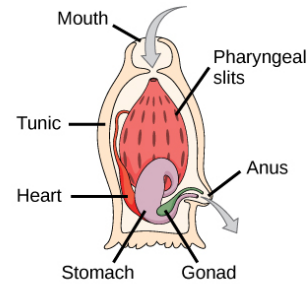
(a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. (c) In the adult stage, the notochord, nerve cord, and tail disappear. (credit: modification of work by Dann Blackwood, USGS)

Most tunicates live a sessile existence on the ocean floor and are suspension feeders. The primary foods of tunicates are plankton and detritus. Seawater enters the tunicate's body through its incurrent siphon. Suspended material is filtered out of this water by a mucous net (pharyngeal slits) and is passed into the intestine via the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water. Tunicates are found in shallow ocean waters around the world.

Cephalochordata

Members of **Cephalochordata** possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage ([link]). The notochord extends into the head, which gives the subphylum its name. Extinct members of this subphylum include *Pikaia*, which is the oldest known cephalochordate. *Pikaia* fossils were recovered from the Burgess shales of Canada and dated to the middle of the Cambrian age, making them more than 500 million years old.

Extant members of Cephalochordata are the **lancelets**, named for their blade-like shape. Lancelets are only a few centimeters long and are usually found buried in sand at the bottom of warm temperate and tropical seas. Like tunicates, they are suspension feeders.
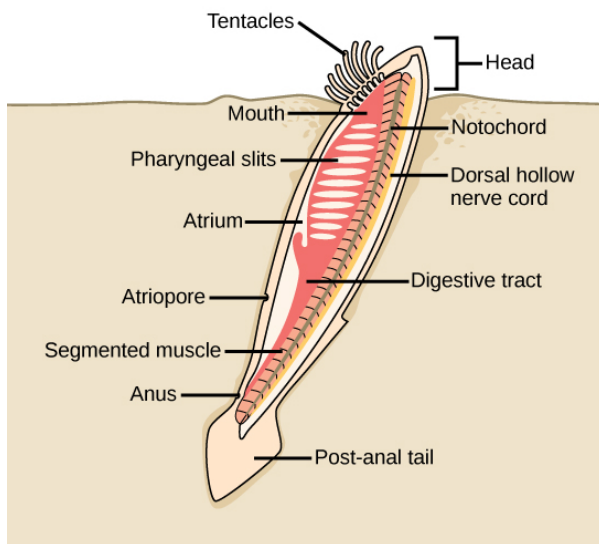
The lancelet, like all cephalochordates, has a head. Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Water from the mouth enters the pharyngeal slits, which filter out food particles. The filtered water

then collects in the atrium and
exits through the atriopore.

Craniata and Vertebrata

A **cranium** is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones ([link]). Most bilaterally symmetrical animals have a head; of these, those that have a cranium compose the clade **Craniata**. Craniata includes the hagfishes (Myxini), which have a cranium but lack a backbone, and all of the organisms called "vertebrates."
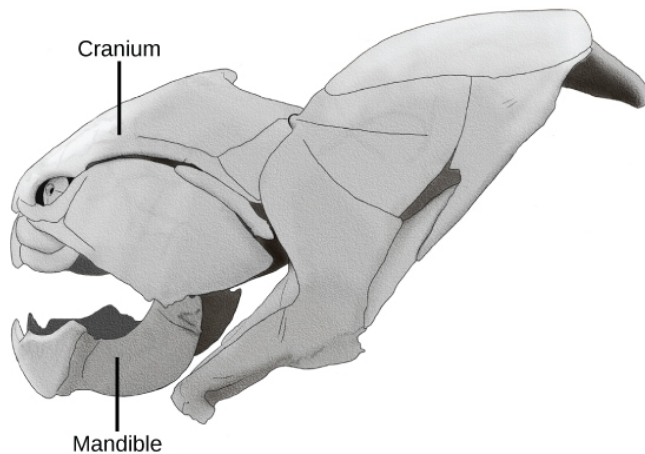
Craniata, including this fish (*Dunkleosteus* sp.), are characterized by the presence of a cranium, mandible, and other facial bones. (credit: "Steveoc 86"/Wikimedia Commons)

Vertebrates are members of the clade **Vertebrata**. Vertebrates display the four characteristic features of the chordates; however, members of this

group also share derived characteristics that distinguish them from invertebrate chordates. Vertebrata is named for the **vertebral column**, composed of vertebrae, a series of separate bones joined together as a backbone ([link]). In adult vertebrates, the vertebral column replaces the notochord, which is only seen in the embryonic stage.
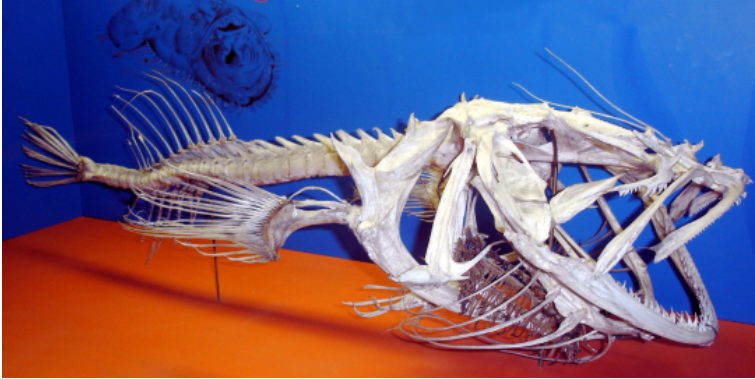
Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium. (credit: Ernest V. More; taken at Smithsonian Museum of Natural History, Washington, D.C.)

Based on molecular analysis, vertebrates appear to be more closely related to lancelets (cephalochordates) than to tunicates (urochordates) among the invertebrate chordates. This evidence suggests that the cephalochordates diverged from Urochordata and the vertebrates subsequently diverged from the cephalochordates. This hypothesis is further supported by the discovery of a fossil in China from the genus *Haikouella*. This organism seems to be an intermediate form between cephalochordates and vertebrates. The *Haikouella* fossils are about 530 million years old and appear similar to modern lancelets. These organisms had a brain and eyes, as do vertebrates, but lack the skull found in craniates.[footnote] This evidence suggests that

vertebrates arose during the Cambrian explosion. Recall that the "Cambrian explosion" is the name given to a relatively brief span of time during the Cambrian period during which many animal groups appeared and rapidly diversified. Most modern animal phyla originated during the Cambrian explosion.

Chen, J. Y., Huang, D. Y., and Li, C. W., "An early Cambrian craniate-like chordate," *Nature* 402 (1999): 518–522, doi:10.1038/990080.

Vertebrates are the largest group of chordates, with more than 62,000 living species. Vertebrates are grouped based on anatomical and physiological traits. More than one classification and naming scheme is used for these animals. Here we will consider the traditional groups Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia, which constitute classes in the subphylum Vertebrata. Many modern authors classify birds within Reptilia, which correctly reflects their evolutionary heritage. We consider them separately only for convenience. Further, we will consider hagfishes and lampreys together as jawless fishes, the agnathans, although emerging classification schemes separate them into chordate jawless fishes (the hagfishes) and vertebrate jawless fishes (the lampreys).

Animals that possess jaws are known as gnathostomes, which means "jawed mouth." Gnathostomes include fishes and tetrapods—amphibians, reptiles, birds, and mammals. Tetrapods can be further divided into two groups: amphibians and amniotes. Amniotes are animals whose eggs are adapted for terrestrial living, and this group includes mammals, reptiles, and birds. Amniotic embryos, developing in either an externally shed egg or an egg carried by the female, are provided with a water-retaining environment and are protected by amniotic membranes.

Section Summary

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension

feeders that feed on phytoplankton and other microorganisms. Vertebrata is named for the vertebral column, which is a feature of almost all members of this clade.

Art Connections

Exercise:

Problem:

[link] Which of the following statements about common features of chordates is true?

 a. The dorsal hollow nerve cord is part of the chordate central nervous system.
 b. In vertebrate fishes, the pharyngeal slits become the gills.
 c. Humans are not chordates because humans do not have a tail.
 d. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

Solution:

[link] A

Review Questions

Exercise:

Problem:

Which of the following is *not* contained in phylum Chordata?

 a. Cephalochordata
 b. Echinodermata
 c. Urochordata
 d. Vertebrata

Solution:

B

Exercise:

Problem:

Which group of invertebrates is most closely related to vertebrates?

   a. cephalochordates
   b. echinoderms
   c. arthropods
   d. urochordates

Solution:

A

Free Response

Exercise:

Problem: What are the characteristic features of the chordates?

Solution:

The characteristic features of the phylum Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

Glossary

Cephalochordata
   chordate clade whose members possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage

Chordata
     phylum of animals distinguished by their possession of a notochord, a
     dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail at some
     point during their development

Craniata
     clade composed of chordates that possess a cranium; includes
     Vertebrata together with hagfishes

cranium
     bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and
     facial bones

dorsal hollow nerve cord
     hollow, tubular structure derived from ectoderm, which is located
     dorsal to the notochord in chordates

lancelet
     member of Cephalochordata; named for its blade-like shape

notochord
     flexible, rod-shaped support structure that is found in the embryonic
     stage of all chordates and in the adult stage of some chordates

pharyngeal slit
     opening in the pharynx

post-anal tail
     muscular, posterior elongation of the body extending beyond the anus
     in chordates

tetrapod
     phylogenetic reference to an organism with a four-footed evolutionary
     history; includes amphibians, reptiles, birds, and mammals

tunicate
     sessile chordate that is a member of Urochordata

Urochordata
    clade composed of tunicates

vertebral column
    series of separate bones joined together as a backbone

Vertebrata
    members of the phylum Chordata that possess a backbone

Fishes
By the end of this section, you will be able to:

- Describe the difference between jawless and jawed fishes
- Discuss the distinguishing features of sharks and rays compared to other modern fishes

Modern fishes include an estimated 31,000 species. Fishes were the earliest vertebrates, with jawless species being the earliest and jawed species evolving later. They are active feeders, rather than sessile, suspension feeders. Jawless fishes—the hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, distinguishing them from the invertebrate chordates.

Jawless Fishes

Jawless fishes are craniates that represent an ancient vertebrate lineage that arose over one half-billion years ago. In the past, the hagfishes and lampreys were classified together as agnathans. Today, hagfishes and lampreys are recognized as separate clades, primarily because lampreys are true vertebrates, whereas hagfishes are not. A defining feature is the lack of paired lateral appendages (fins). Some of the earliest jawless fishes were the **ostracoderms** (which translates to "shell-skin"). Ostracoderms were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

Myxini: Hagfishes

The clade **Myxini** includes at least 20 species of hagfishes. **Hagfishes** are eel-like scavengers that live on the ocean floor and feed on dead invertebrates, other fishes, and marine mammals ([link]). Hagfishes are entirely marine and are found in oceans around the world, except for the polar regions. A unique feature of these animals is the slime glands beneath the skin that release mucus through surface pores. This mucus allows the hagfish to escape from the grip of predators. Hagfish can also twist their bodies in a knot to feed and sometimes eat carcasses from the inside out.

Pacific hagfish are scavengers that live on the ocean floor. (credit: Linda Snook, NOAA/CBNMS)

The skeleton of a hagfish is composed of cartilage, which includes a cartilaginous notochord that runs the length of the body. This notochord provides support to the hagfish's body. Hagfishes do not replace the notochord with a vertebral column during development, as do true vertebrates.

Petromyzontidae: Lampreys

The clade **Petromyzontidae** includes approximately 35–40 or more species of lampreys. **Lampreys** are similar to hagfishes in size and shape; however, lampreys possess some vertebral elements. Lampreys lack paired appendages and bone, as do the hagfishes. As adults, lampreys are characterized by a toothed, funnel-like sucking mouth. Many species have a parasitic stage of their life cycle during which they are ectoparasites of fishes ([link]).

These parasitic sea lampreys attach to their lake trout host by suction and use their rough tongues to rasp away flesh in order to feed on the trout's blood. (credit: USGS)

Lampreys live primarily in coastal and fresh waters, and have a worldwide distribution, except for in the tropics and polar regions. Some species are marine, but all species spawn in fresh water. Eggs are fertilized externally, and the larvae distinctly differ from the adult form, spending 3 to 15 years as suspension feeders. Once they attain sexual maturity, the adults reproduce and die within days.

Lampreys possess a notochord as adults; however, this notochord is surrounded by a cartilaginous structure called an arcualia, which may resemble an evolutionarily early form of the vertebral column.

Gnathostomes: Jawed Fishes

Gnathostomes or "jaw-mouths" are vertebrates that possess jaws. One of the most significant developments in early vertebrate evolution was the development of the jaw, which is a hinged structure attached to the cranium that allows an animal to grasp and tear its food. The evolution of jaws

allowed early gnathostomes to exploit food resources that were unavailable to jawless fishes.

Early gnathostomes also possessed two sets of paired fins, allowing the fishes to maneuver accurately. Pectoral fins are typically located on the anterior body, and pelvic fins on the posterior. Evolution of the jaw and paired fins permitted gnathostomes to expand from the sedentary suspension feeding of jawless fishes to become mobile predators. The ability of gnathostomes to exploit new nutrient sources likely is one reason that they replaced most jawless fishes during the Devonian period. Two early groups of gnathostomes were the acanthodians and placoderms ([link]), which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes.

Dunkleosteous was an enormous placoderm from the Devonian period, 380–360 million years ago. It measured up to 10 meters in length and weighed up to 3.6 tons. (credit: Nobu Tamura)

Chondrichthyes: Cartilaginous Fishes

The clade **Chondrichthyes** is diverse, consisting of sharks ([link]), rays, and skates, together with sawfishes and a few dozen species of fishes called *chimaeras*, or "ghost" sharks." Chondrichthyes are jawed fishes that possess paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the early or middle Devonian. They are thought to be descended from the placoderms, which had skeletons made of bone; thus, the cartilaginous skeleton of Chondrichthyes is a later development. Parts of shark skeleton are strengthened by granules of calcium carbonate, but this is not the same as bone.

Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for a part or all of their lives. Most sharks are carnivores that feed on live prey, either swallowing it whole or using their jaws and teeth to tear it into smaller pieces. Shark teeth likely evolved from the jagged scales that cover their skin, called placoid scales. Some species of sharks and rays are suspension feeders that feed on plankton.

Hammerhead sharks tend to school during the day and hunt prey at night. (credit: Masashi Sugawara)

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and electroreception, with the latter perhaps the most sensitive of any animal. Organs called **ampullae of Lorenzini** allow sharks to detect the electromagnetic fields that are produced by all living things, including their prey. Electroreception has only been observed in aquatic or amphibious animals. Sharks, together with most fishes and aquatic and larval amphibians, also have a sense organ called the **lateral line**, which is used to detect movement and vibration in the surrounding water, and is often considered homologous to "hearing" in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of a fish's body.

Sharks reproduce sexually, and eggs are fertilized internally. Most species are ovoviviparous: The fertilized egg is retained in the oviduct of the mother's body and the embryo is nourished by the egg yolk. The eggs hatch in the uterus, and young are born alive and fully functional. Some species of sharks are oviparous: They lay eggs that hatch outside of the mother's body. Embryos are protected by a shark egg case or "mermaid's purse" ([link]) that has the consistency of leather. The shark egg case has tentacles that snag in seaweed and give the newborn shark cover. A few species of sharks are viviparous: The young develop within the mother's body and she gives live birth.
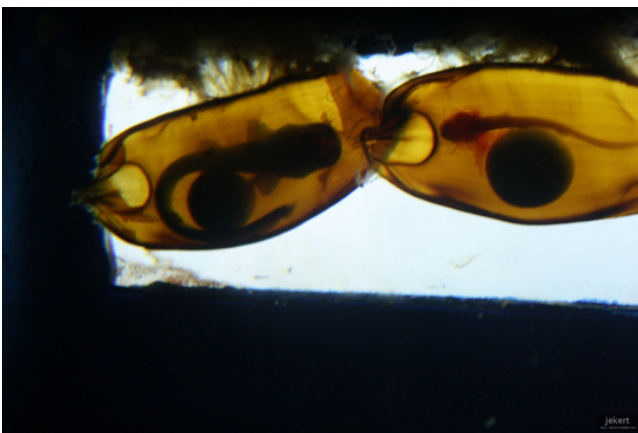
Shark embryos are clearly visible
through these transparent egg

cases. The round structure is the
yolk that nourishes the growing
embryo. (credit: Jek Bacarisas)

Rays and skates comprise more than 500 species and are closely related to sharks. They can be distinguished from sharks by their flattened bodies, pectoral fins that are enlarged and fused to the head, and gill slits on their ventral surface ([link]). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.

This stingray blends into the sandy
bottom of the ocean floor. (credit:
"Sailn1"/Flickr)

Osteichthyes: Bony Fishes

Members of the clade **Osteichthyes**, also called bony fishes, are characterized by a bony skeleton. The vast majority of present-day fishes belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fishes have an ossified skeleton with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. This characteristic has only reversed in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered by overlapping scales, and glands in the skin secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fishes have a lateral line system that detects vibrations in water.

All bony fishes use gills to breathe. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Many bony fishes also have a **swim bladder**, a gas-filled organ that helps to control the buoyancy of the fish. Bony fishes are further divided into two extant clades: **Actinopterygii** (ray-finned fishes) and **Sarcopterygii** (lobe-finned fishes).

Actinopterygii, the ray-finned fishes, include many familiar fishes—tuna, bass, trout, and salmon ([link]**a**), among others. Ray-finned fishes are named for their fins that are webs of skin supported by bony spines called rays. In contrast, the fins of Sarcopterygii are fleshy and lobed, supported by bone ([link]**b**). Living members of this clade include the less-familiar lungfishes and coelacanths.

(a)   (b)
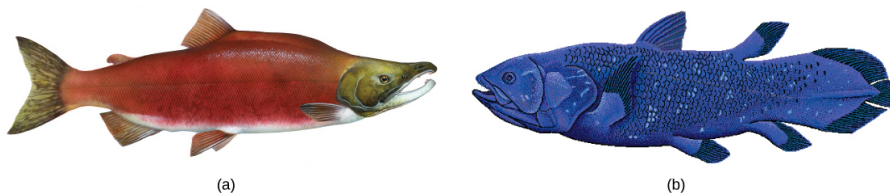
The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish,

was thought to have gone extinct in the Late Cretaceous period, 100 million years ago, until one was discovered in 1938 near the Comoros Islands between Africa and Madagascar. (credit a: modification of work by Timothy Knepp, USFWS; credit b: modification of work by Robbie Cada)

Section Summary

The earliest vertebrates that diverged from the invertebrate chordates were the jawless fishes. Fishes with jaws (gnathostomes) evolved later. Jaws allowed early gnathostomes to exploit new food sources. Agnathans include the hagfishes and lampreys. Hagfishes are eel-like scavengers that feed on dead invertebrates and other fishes. Lampreys are characterized by a toothed, funnel-like sucking mouth, and most species are parasitic on other fishes. Gnathostomes include the cartilaginous fishes and the bony fishes, as well as all other tetrapods. Cartilaginous fishes include sharks, rays, skates, and ghost sharks. Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for part or all of their lives. The vast majority of present-day fishes belong to the clade Osteichthyes, which consists of approximately 30,000 species. Bony fishes can be divided into two clades: Actinopterygii (ray-finned fishes, virtually all extant species) and Sarcopterygii (lobe-finned fishes, comprising fewer than 10 extant species but which are the ancestors of tetrapods).

Review Questions

Exercise:

Problem:

Members of Chondrichthyes differ from members of Osteichthyes by having a _____.

a. jaw

b. bony skeleton
c. cartilaginous skeleton
d. two sets of paired fins

Solution:

C

Exercise:

Problem:

Members of Chondrichthyes are thought to be descended from fishes that had _____.

a. a cartilaginous skeleton
b. a bony skeleton
c. mucus glands
d. slime glands

Solution:

B

Free Response

Exercise:

Problem:

What can be inferred about the evolution of the cranium and vertebral column from examining hagfishes and lampreys?

Solution:

Comparison of hagfishes with lampreys shows that the cranium evolved first in early vertebrates, as it is seen in hagfishes, which

evolved earlier than lampreys. This was followed by evolution of the vertebral column, a primitive form of which is seen in lampreys and not in hagfishes.

Exercise:

Problem: Why did gnathostomes replace most agnathans?

Solution:

Evolution of the jaw and paired fins permitted gnathostomes to diversify from the sedentary suspension feeding of agnathans to a mobile predatory lifestyle. The ability of gnathostomes to utilize new nutrient sources may be one reason why the gnathostomes replaced most agnathans.

Glossary

Actinopterygii
    ray-finned fishes

ampulla of Lorenzini
    sensory organ that allows sharks to detect electromagnetic fields produced by living things

Chondrichthyes
    jawed fish with paired fins and a skeleton made of cartilage

gnathostome
    jawed fish

hagfish
    eel-like jawless fish that live on the ocean floor and are scavengers

lamprey
    jawless fish characterized by a toothed, funnel-like, sucking mouth

lateral line
	sense organ that runs the length of a fish's body; used to detect vibration in the water

Myxini
	hagfishes

Osteichthyes
	bony fish

ostracoderm
	one of the earliest jawless fish covered in bone

Petromyzontidae
	clade of lampreys

Sarcopterygii
	lobe-finned fish

swim bladder
	in fishes, a gas filled organ that helps to control the buoyancy of the fish

Amphibians
By the end of this section, you will be able to:

- Describe the important difference between the life cycle of amphibians and the life cycles of other vertebrates
- Distinguish between the characteristics of Urodela, Anura, and Apoda
- Describe the evolutionary history of amphibians

Amphibians are vertebrate tetrapods. **Amphibia** includes frogs, salamanders, and caecilians. The term amphibian loosely translates from the Greek as "dual life," which is a reference to the metamorphosis that many frogs and salamanders undergo and their mixture of aquatic and terrestrial environments in their life cycle. Amphibians evolved during the Devonian period and were the earliest terrestrial tetrapods.

Characteristics of Amphibians

As tetrapods, most amphibians are characterized by four well-developed limbs. Some species of salamanders and all caecilians are functionally limbless; their limbs are vestigial. An important characteristic of extant amphibians is a moist, permeable skin that is achieved via mucus glands that keep the skin moist; thus, exchange of oxygen and carbon dioxide with the environment can take place through it (**cutaneous respiration**). Additional characteristics of amphibians include pedicellate teeth—teeth in which the root and crown are calcified, separated by a zone of noncalcified tissue—and a papilla amphibiorum and papilla basilaris, structures of the inner ear that are sensitive to frequencies below and above 10,00 hertz, respectively. Amphibians also have an auricular operculum, which is an extra bone in the ear that transmits sounds to the inner ear. All extant adult amphibians are carnivorous, and some terrestrial amphibians have a sticky tongue that is used to capture prey.

Evolution of Amphibians

The fossil record provides evidence of the first tetrapods: now-extinct amphibian species dating to nearly 400 million years ago. Evolution of tetrapods from fishes represented a significant change in body plan from one suited to organisms that respired and swam in water, to organisms that breathed air and moved onto land; these changes occurred over a span of 50 million years during the Devonian period. One of the earliest known tetrapods is from the genus *Acanthostega*. *Acanthostega* was aquatic; fossils show that it had gills similar to fishes. However, it also had four limbs, with the skeletal structure of limbs found in present-day tetrapods, including amphibians. Therefore, it is thought that *Acanthostega* lived in shallow waters and was an intermediate form between lobe-finned fishes and early, fully terrestrial tetrapods. What preceded *Acanthostega*?

In 2006, researchers published news of their discovery of a fossil of a "tetrapod-like fish," *Tiktaalik roseae*, which seems to be an intermediate form between fishes having fins and tetrapods having limbs ([link]). *Tiktaalik* likely lived in a shallow water environment about 375 million years ago.[footnote]

Daeschler, E. B., Shubin, N. H., and Jenkins, F. J. "A Devonian tetrapod-like fish and the evolution of the tetrapod body plan," *Nature* 440 (2006): 757–763, doi:10.1038/nature04639, http://www.nature.com/nature/journal/v440/n7085/abs/nature04639.html.
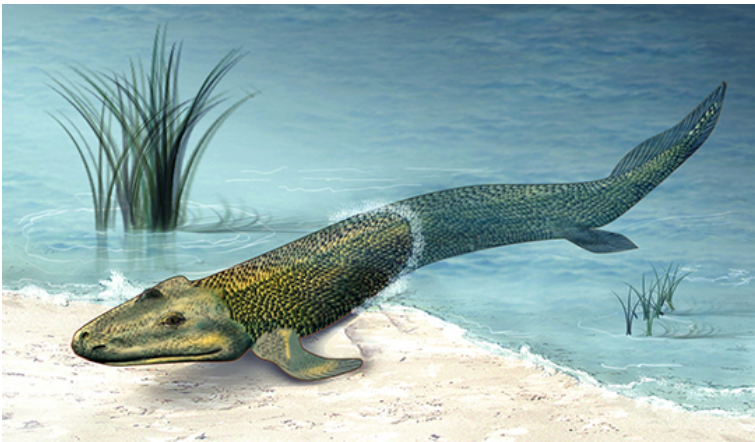
The recent fossil discovery of *Tiktaalik roseae* suggests evidence for an animal intermediate to finned fish and legged tetrapods. (credit: Zina Deretsky, National Science Foundation)

The early tetrapods that moved onto land had access to new nutrient sources and relatively few predators. This led to the widespread distribution of tetrapods during the early Carboniferous period, a period sometimes called the "age of the amphibians."

Modern Amphibians

Amphibia comprises an estimated 6,770 extant species that inhabit tropical and temperate regions around the world. Amphibians can be divided into three clades: **Urodela** ("tailed-ones"), the salamanders; **Anura** ("tail-less ones"), the frogs; and **Apoda** ("legless ones"), the caecilians.

Urodela: Salamanders

Salamanders are amphibians that belong to the order Urodela. Living salamanders ([link]) include approximately 620 species, some of which are aquatic, other terrestrial, and some that live on land only as adults. Adult salamanders usually have a generalized tetrapod body plan with four limbs and a tail. They move by bending their bodies from side to side, called lateral undulation, in a fish-like manner while "walking" their arms and legs fore and aft. It is thought that their gait is similar to that used by early tetrapods. Respiration differs among different species. The majority of salamanders are lungless, and respiration occurs through the skin or through external gills. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs.

Unlike frogs, virtually all salamanders rely on internal fertilization of the eggs. The only male amphibians that possess copulatory structures are the caecilians, so fertilization among salamanders typically involves an elaborate and often prolonged courtship. Such a courtship allows the successful transfer of sperm from male to female via a spermatophore. Development in many of the most highly evolved salamanders, which are fully terrestrial, occurs during a prolonged egg stage, with the eggs guarded by the mother. During this time, the gilled larval stage is found only within the egg capsule, with the gills being resorbed, and metamorphosis being completed, before hatching. Hatchlings thus resemble tiny adults.

Most salamanders have legs and a tail, but respiration varies among species. (credit: Valentina Storti)

Anura: Frogs

Frogs are amphibians that belong to the order Anura ([link]). Anurans are among the most diverse groups of vertebrates, with approximately 5,965 species that occur on all of the continents except Antarctica. Anurans have a

body plan that is more specialized for movement. Adult frogs use their hind limbs to jump on land. Frogs have a number of modifications that allow them to avoid predators, including skin that acts as camouflage. Many species of frogs and salamanders also release defensive chemicals from glands in the skin that are poisonous to predators.

The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source.

Frog eggs are fertilized externally, and like other amphibians, frogs generally lay their eggs in moist environments. A moist environment is required as eggs lack a shell and thus dehydrate quickly in dry environments. Frogs demonstrate a great diversity of parental behaviors, with some species laying many eggs and exhibiting little parental care, to species that carry eggs and tadpoles on their hind legs or backs. The life cycle of frogs, as other amphibians, consists of two distinct stages: the larval stage followed by metamorphosis to an adult stage. The larval stage of a frog, the **tadpole**, is often a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, and lack limbs. At the end of the tadpole stage, frogs undergo metamorphosis into the adult form ([link]). During this stage, the gills, tail, and lateral line system disappear,

and four limbs develop. The jaws become larger and are suited for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop. These changes during metamorphosis allow the larvae to move onto land in the adult stage.

A juvenile frog metamorphoses into a frog. Here, the frog has started to develop limbs, but its tadpole tail is still evident.

Apoda: Caecilians

An estimated 185 species comprise **caecilians**, a group of amphibians that belong to the order Apoda. Although they are vertebrates, a complete lack of limbs leads to their resemblance to earthworms in appearance. They are adapted for a soil-burrowing or aquatic lifestyle, and they are nearly blind. These animals are found in the tropics of South America, Africa, and Southern Asia. They have vestigial limbs, evidence that they evolved from a legged ancestor.

Evolution Connection

The Paleozoic Era and the Evolution of Vertebrates

The climate and geography of Earth was vastly different during the Paleozoic Era, when vertebrates arose, as compared to today. The Paleozoic spanned from approximately 542 to 251 million years ago. The landmasses on Earth were very different from those of today. Laurentia and Gondwana were continents located near the equator that subsumed much of the current day landmasses in a different configuration ([link]). At this time, sea levels were very high, probably at a level that hasn't been reached since. As the Paleozoic progressed, glaciations created a cool global climate, but conditions warmed near the end of the first half of the Paleozoic. During the latter half of the Paleozoic, the landmasses began moving together, with the initial formation of a large northern block called Laurasia. This contained parts of what is now North America, along with Greenland, parts of Europe, and Siberia. Eventually, a single supercontinent, called Pangaea, was formed, starting in the latter third of the Paleozoic. Glaciations then began to affect Pangaea's climate, affecting the distribution of vertebrate life.
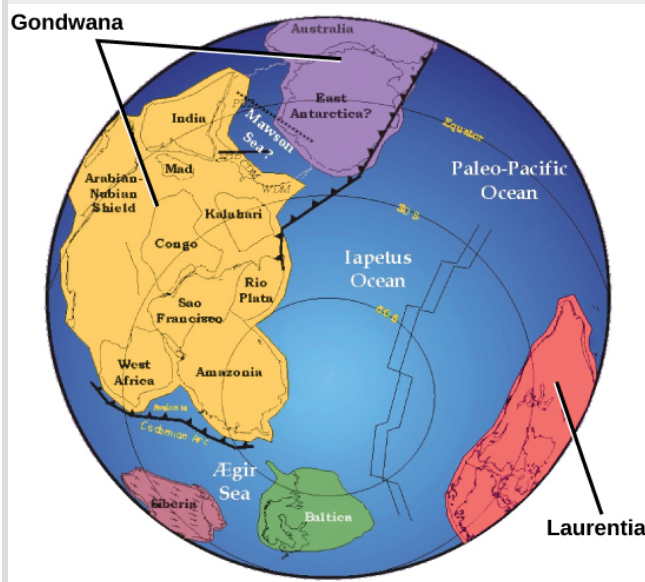
During the Paleozoic Era, around 550 million years ago, the continent Gondwana formed. Both Gondwana and the continent

Laurentia were located near the equator.

During the early Paleozoic, the amount of carbon dioxide in the atmosphere was much greater than it is today. This may have begun to change later, as land plants became more common. As the roots of land plants began to infiltrate rock and soil began to form, carbon dioxide was drawn out of the atmosphere and became trapped in the rock. This reduced the levels of carbon dioxide and increased the levels of oxygen in the atmosphere, so that by the end of the Paleozoic, atmospheric conditions were similar to those of today.

As plants became more common through the latter half of the Paleozoic, microclimates began to emerge and ecosystems began to change. As plants and ecosystems continued to grow and become more complex, vertebrates moved from the water to land. The presence of shoreline vegetation may have contributed to the movement of vertebrates onto land. One hypothesis suggests that the fins of aquatic vertebrates were used to maneuver through this vegetation, providing a precursor to the movement of fins on land and the development of limbs. The late Paleozoic was a time of diversification of vertebrates, as amniotes emerged and became two different lines that gave rise, on one hand, to mammals, and, on the other hand, to reptiles and birds. Many marine vertebrates became extinct near the end of the Devonian period, which ended about 360 million years ago, and both marine and terrestrial vertebrates were decimated by a mass extinction in the early Permian period about 250 million years ago.

Note:
Link to Learning

Section Summary

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians are limbless. The most important characteristic of extant amphibians is a moist, permeable skin used for cutaneous respiration. The fossil record provides evidence of amphibian species, now extinct, that arose over 400 million years ago as the first tetrapods. Amphibia can be divided into three clades: salamanders (Urodela), frogs (Anura), and caecilians (Apoda). The life cycle of frogs, like the majority of amphibians, consists of two distinct stages: the larval stage and metamorphosis to an adult stage. Some species in all orders bypass a free-living larval stage.

Review Questions

Exercise:

Problem: Which of the following is *not* true of *Acanthostega*?

a. It was aquatic.
b. It had gills.
c. It had four limbs.
d. It laid shelled eggs.

Solution:

D

Exercise:

Problem: Frogs belong to which order?

a. Anura
b. Urodela
c. Caudata
d. Apoda

Solution:

A

Free Response

Exercise:

Problem: Explain why frogs are restricted to a moist environment.

Solution:

A moist environment is required, as frog eggs lack a shell and dehydrate quickly in dry environments.

Exercise:

Problem:

Describe the differences between the larval and adult stages of frogs.

Solution:

The larval stage of frogs is the tadpole, which is usually a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, and lack limbs. In the adult form, the gills and lateral line system disappear, and four limbs develop. The jaws grow larger, suitable for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop.

Glossary

Acanthostega
    one of the earliest known tetrapods

Amphibia
    frogs, salamanders, and caecilians

Anura
    frogs

Apoda
    caecilians

caecilian
    legless amphibian that belongs to the clade Apoda

cutaneous respiration
    gas exchange through the skin

frog
    tail-less amphibian that belongs to the clade Anura

salamander
    tailed amphibian that belongs to the clade Urodela

tadpole
    larval stage of a frog

Urodela
    salamanders

Reptiles
By the end of this section, you will be able to:

- Describe the main characteristics of amniotes
- Explain the difference between anapsids, synapsids, and diapsids, and give an example of each
- Identify the characteristics of reptiles
- Discuss the evolution of reptiles

The amniotes —reptiles, birds, and mammals—are distinguished from amphibians by their terrestrially adapted egg, which is protected by amniotic membranes. The evolution of amniotic membranes meant that the embryos of amniotes were provided with their own aquatic environment, which led to less dependence on water for development and thus allowed the amniotes to branch out into drier environments. This was a significant development that distinguished them from amphibians, which were restricted to moist environments due their shell-less eggs. Although the shells of various amniotic species vary significantly, they all allow retention of water. The shells of bird eggs are composed of calcium carbonate and are hard, but fragile. The shells of reptile eggs are leathery and require a moist environment. Most mammals do not lay eggs (except for monotremes). Instead, the embryo grows within the mother's body; however, even with this internal gestation, amniotic membranes are still present.

Characteristics of Amniotes

The amniotic egg is the key characteristic of amniotes. In amniotes that lay eggs, the shell of the egg provides protection for the developing embryo while being permeable enough to allow for the exchange of carbon dioxide and oxygen. The albumin, or egg white, provides the embryo with water and protein, whereas the fattier egg yolk is the energy supply for the embryo, as is the case with the eggs of many other animals, such as amphibians. However, the eggs of amniotes contain three additional extra-embryonic membranes: the chorion, amnion, and allantois ([link]). Extra-embryonic membranes are membranes present in amniotic eggs that are not a part of the body of the developing embryo. While the inner amniotic membrane surrounds the embryo itself, the **chorion** surrounds the embryo

and yolk sac. The chorion facilitates exchange of oxygen and carbon dioxide between the embryo and the egg's external environment. The **amnion** protects the embryo from mechanical shock and supports hydration. The **allantois** stores nitrogenous wastes produced by the embryo and also facilitates respiration. In mammals, membranes that are homologous to the extra-embryonic membranes in eggs are present in the placenta.

Note:
Art Connection
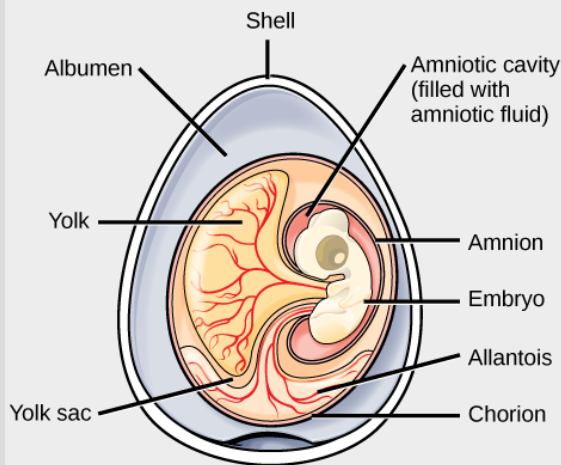
The key features of an amniotic egg are shown.

Which of the following statements about the parts of an egg are false?

a. The allantois stores nitrogenous waste and facilitates respiration.
b. The chorion facilitates gas exchange.
c. The yolk provides food for the growing embryo.
d. The amniotic cavity is filled with albumen.

Additional derived characteristics of amniotes include waterproof skin, due to the presence of lipids, and costal (rib) ventilation of the lungs.

Evolution of Amniotes

The first amniotes evolved from amphibian ancestors approximately 340 million years ago during the Carboniferous period. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids and sauropsids. **Synapsids** include all mammals, including extinct mammalian species. Synapsids also include therapsids, which were mammal-like reptiles from which mammals evolved. **Sauropsids** include reptiles and birds, and can be further divided into anapsids and diapsids. The key differences between the synapsids, anapsids, and diapsids are the structures of the skull and the number of temporal fenestrae behind each eye ([link]). **Temporal fenestrae** are post-orbital openings in the skull that allow muscles to expand and lengthen. **Anapsids** have no temporal fenestrae, synapsids have one, and **diapsids** have two. Anapsids include extinct organisms and may, based on anatomy, include turtles. However, this is still controversial, and turtles are sometimes classified as diapsids based on molecular evidence. The diapsids include birds and all other living and extinct reptiles.

Anapsid skull   Synapsid skull   Diapsid skull
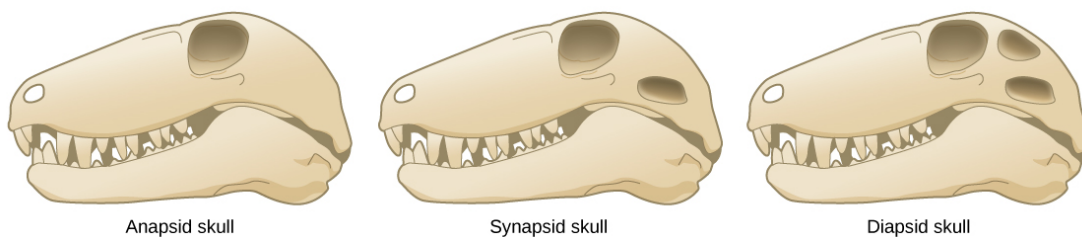
Compare the skulls and temporal fenestrae of anapsids, synapsids, and diapsids. Anapsids have no openings, synapsids have one opening, and diapsids have two openings.

The diapsids diverged into two groups, the Archosauromorpha ("ancient lizard form") and the Lepidosauromorpha ("scaly lizard form") during the Mesozoic period ([link]). The **lepidosaurs** include modern lizards, snakes, and tuataras. The **archosaurs** include modern crocodiles and alligators, and the extinct pterosaurs ("winged lizard") and dinosaurs ("terrible lizard"). Clade Dinosauria includes birds, which evolved from a branch of dinosaurs.

Note:
Art Connection
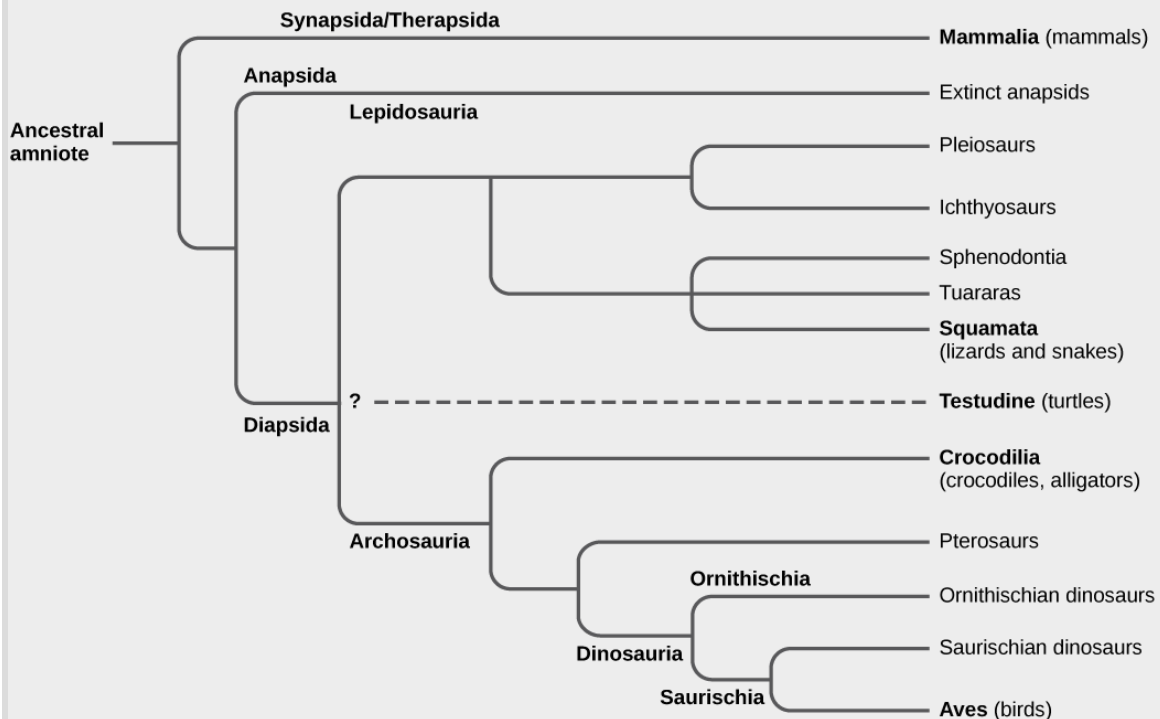
This chart shows the evolution of amniotes. The placement of Testudines (turtles) is currently still debated.

Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

In the past, the most common division of amniotes has been into the classes Mammalia, Reptilia, and Aves. Birds are descended, however, from dinosaurs, so this classical scheme results in groups that are not true clades. We will consider birds as a group distinct from reptiles for the purpose of this discussion with the understanding that this does not completely reflect phylogenetic history and relationships.

Characteristics of Reptiles

Reptiles are tetrapods. Limbless reptiles—snakes and other squamates—have vestigial limbs and, like caecilians, are classified as tetrapods because they are descended from four-limbed ancestors. Reptiles lay eggs enclosed in shells on land. Even aquatic reptiles return to the land to lay eggs. They usually reproduce sexually with internal fertilization. Some species display ovoviviparity, with the eggs remaining in the mother's body until they are ready to hatch. Other species are viviparous, with the offspring born alive.

One of the key adaptations that permitted reptiles to live on land was the development of their scaly skin, containing the protein keratin and waxy lipids, which reduced water loss from the skin. This occlusive skin means that reptiles cannot use their skin for respiration, like amphibians, and thus all breathe with lungs.

Reptiles are ectotherms, animals whose main source of body heat comes from the environment. This is in contrast to endotherms, which use heat produced by metabolism to regulate body temperature. In addition to being ectothermic, reptiles are categorized as poikilotherms, or animals whose body temperatures vary rather than remain stable. Reptiles have behavioral adaptations to help regulate body temperature, such as basking in sunny places to warm up and finding shady spots or going underground to cool down. The advantage of ectothermy is that metabolic energy from food is not required to heat the body; therefore, reptiles can survive on about 10 percent of the calories required by a similarly sized endotherm. In cold weather, some reptiles such as the garter snake brumate. **Brumation** is similar to hibernation in that the animal becomes less active and can go for long periods without eating, but differs from hibernation in that brumating

reptiles are not asleep or living off fat reserves. Rather, their metabolism is slowed in response to cold temperatures, and the animal is very sluggish.

Evolution of Reptiles

Reptiles originated approximately 300 million years ago during the Carboniferous period. One of the oldest known amniotes is **Casineria**, which had both amphibian and reptilian characteristics. One of the earliest undisputed reptiles was **Hylonomus**. Soon after the first amniotes appeared, they diverged into three groups—synapsids, anapsids, and diapsids—during the Permian period. The Permian period also saw a second major divergence of diapsid reptiles into archosaurs (predecessors of crocodilians and dinosaurs) and lepidosaurs (predecessors of snakes and lizards). These groups remained inconspicuous until the Triassic period, when the archosaurs became the dominant terrestrial group due to the extinction of large-bodied anapsids and synapsids during the Permian-Triassic extinction. About 250 million years ago, archosaurs radiated into the dinosaurs and the pterosaurs.

Although they are sometimes mistakenly called dinosaurs, the pterosaurs were distinct from true dinosaurs ([link]). Pterosaurs had a number of adaptations that allowed for flight, including hollow bones (birds also exhibit hollow bones, a case of convergent evolution). Their wings were formed by membranes of skin that attached to the long, fourth finger of each arm and extended along the body to the legs.

Pterosaurs, which existed from the late Triassic to the Cretaceous period (210 to 65.5 million years ago), possessed wings but are not believed to have been capable of powered flight. Instead, they may have been able to soar after launching from cliffs. (credit: Mark Witton, Darren Naish)

The dinosaurs were a diverse group of terrestrial reptiles with more than 1,000 species identified to date. Paleontologists continue to discover new species of dinosaurs. Some dinosaurs were quadrupeds ([link]); others were bipeds. Some were carnivorous, whereas others were herbivorous. Dinosaurs laid eggs, and a number of nests containing fossilized eggs have been found. It is not known whether dinosaurs were endotherms or ectotherms. However, given that modern birds are endothermic, the dinosaurs that served as ancestors to birds likely were endothermic as well. Some fossil evidence exists for dinosaurian parental care, and comparative biology supports this hypothesis since the archosaur birds and crocodilians display parental care.
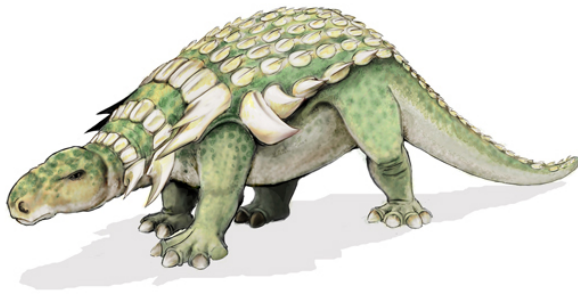
Edmontonia was an armored dinosaur that lived in the late Cretaceous period, 145.5 to 65.6 million years ago. (credit: Mariana Ruiz Villareal)

Dinosaurs dominated the Mesozoic Era, which was known as the "age of reptiles." The dominance of dinosaurs lasted until the end of the Cretaceous, the last period of the Mesozoic Era. The Cretaceous-Tertiary extinction resulted in the loss of most of the large-bodied animals of the Mesozoic Era. Birds are the only living descendants of one of the major clades of dinosaurs.

Note:
Link to Learning

Visit this site to see a video discussing the hypothesis that an asteroid caused the Cretaceous-Triassic (KT) extinction.

Modern Reptiles

Class Reptilia includes many diverse species that are classified into four living clades. These are the 25 species of Crocodilia, 2 species of Sphenodontia, approximately 9,200 Squamata species, and the Testudines, with about 325 species.

Crocodilia

Crocodilia ("small lizard") arose with a distinct lineage by the middle Triassic; extant species include alligators, crocodiles, and caimans. Crocodilians ([link]) live throughout the tropics and subtropics of Africa, South America, Southern Florida, Asia, and Australia. They are found in freshwater, saltwater, and brackish habitats, such as rivers and lakes, and spend most of their time in water. Some species are able to move on land due to their semi-erect posture.

Crocodilians, such as this Siamese crocodile (*Crocodylus siamensis*), provide parental care for their offspring. (credit: Keshav Mukund Kandhadai)

Sphenodontia

Sphenodontia ("wedge tooth") arose in the Mesozoic era and includes only one living genus, *Tuatara*, comprising two species that are found in New Zealand ([link]). Tuataras measure up to 80 centimeters and weigh about 1 kilogram. Although quite lizard-like in gross appearance, several unique features of the skull and jaws clearly define them and distinguish the group from the squamates.

This tuatara from New Zealand may resemble a lizard but belongs to a distinct lineage, the Sphenodontidae family. (credit: Sid Mosdell)

Squamata

Squamata ("scaly") arose in the late Permian, and extant species include lizards and snakes. Both are found on all continents except Antarctica. Lizards and snakes are most closely related to tuataras, both groups having evolved from a lepidosaurian ancestor. Squamata is the largest extant clade of reptiles ([link]). Most lizards differ from snakes by having four limbs, although these have been variously lost or significantly reduced in at least 60 lineages. Snakes lack eyelids and external ears, which are present in lizards. Lizard species range in size from chameleons and geckos, which are a few centimeters in length, to the Komodo dragon, which is about 3 meters in length. Most lizards are carnivorous, but some large species, such as iguanas, are herbivores.

This Jackson's chameleon (*Trioceros jacksonii*) blends in with its surroundings.

Snakes are thought to have descended from either burrowing lizards or aquatic lizards over 100 million years ago ([link]). Snakes comprise about 3,000 species and are found on every continent except Antarctica. They range in size from 10 centimeter-long thread snakes to 10 meter-long pythons and anacondas. All snakes are carnivorous and eat small animals, birds, eggs, fish, and insects. The snake body form is so specialized that, in

its general morphology, a "snake is a snake." Their specializations all point to snakes having evolved to feed on relatively large prey (even though some current species have reversed this trend). Although variations exist, most snakes have a skull that is very flexible, involving eight rotational joints. They also differ from other squamates by having mandibles (lower jaws) without either bony or ligamentous attachment anteriorly. Having this connection via skin and muscle allows for great expansion of the gape and independent motion of the two sides—both advantages in swallowing big items.

The garter snake belongs to the genus *Thamnophis*, the most widely distributed reptile genus in North America. (credit: Steve Jurvetson)

Testudines

Turtles are members of the clade **Testudines** ("having a shell") ([link]). Turtles are characterized by a bony or cartilaginous shell. The shell consists

of the ventral surface called the plastron and the dorsal surface called the carapace, which develops from the ribs. The plastron is made of scutes or plates; the scutes can be used to differentiate species of turtles. The two clades of turtles are most easily recognized by how they retract their necks. The dominant group, which includes all North American species, retracts its neck in a vertical S-curve. Turtles in the less speciose clade retract the neck with a horizontal curve.

Turtles arose approximately 200 million years ago, predating crocodiles, lizards, and snakes. Similar to other reptiles, turtles are ectotherms. They lay eggs on land, although many species live in or near water. None exhibit parental care. Turtles range in size from the speckled padloper tortoise at 8 centimeters (3.1 inches) to the leatherback sea turtle at 200 centimeters (over 6 feet). The term "turtle" is sometimes used to describe only those species of Testudines that live in the sea, with the terms "tortoise" and "terrapin" used to refer to species that live on land and in fresh water, respectively.

The African spurred tortoise (*Geochelone sulcata*) lives at the southern edge of the Sahara Desert. It is the third largest

tortoise in the world. (credit: Jim
Bowen)

Section Summary

The amniotes are distinguished from amphibians by the presence of a terrestrially adapted egg protected by amniotic membranes. The amniotes include reptiles, birds, and mammals. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids (mammals) and sauropsids. Sauropsids can be further divided into anapsids (turtles) and diapsids (birds and reptiles). Reptiles are tetrapods either having four limbs or descending from such. Limbless reptiles (snakes) are classified as tetrapods, as they are descended from four-limbed organisms. One of the key adaptations that permitted reptiles to live on land was the development of scaly skin containing the protein keratin, which prevented water loss from the skin. Reptilia includes four living clades: Crocodilia (crocodiles and alligators), Sphenodontia (tuataras), Squamata (lizards and snakes), and Testudines (turtles).

Art Connections

Exercise:

Problem:

[link] Which of the following statements about the parts of an egg are false?

a. The allantois stores nitrogenous waste and facilitates respiration.
b. The chorion facilitates gas exchange.
c. The yolk provides food for the growing embryo.
d. The amniotic cavity is filled with albumen.

Solution:

[link] D

Exercise:

Problem:

[link] Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

Solution:

[link] The ancestor of modern Testudines may at one time have had a second opening in the skull, but over time this might have been lost.

Review Questions

Exercise:

Problem: During the Mesozoic period, diapsids diverged into_____.

a. pterosaurs and dinosaurs
b. mammals and reptiles
c. lepidosaurs and archosaurs
d. Testudines and Sphenodontia

Solution:

C

Exercise:

Problem: Squamata includes_____.

a. crocodiles and alligators
b. turtles
c. tuataras
d. lizards and snakes

Solution:

D

Free Response

Exercise:

Problem:

Describe the functions of the three extra-embryonic membranes present in amniotic eggs.

Solution:

The chorion facilitates the exchange of oxygen and carbon dioxide gases between the embryo and the surrounding air. The amnion protects the embryo from mechanical shock and prevents dehydration. The allantois stores nitrogenous wastes produced by the embryo and facilitates respiration.

Exercise:

Problem: What characteristics differentiate lizards and snakes?

Solution:

Lizards differ from snakes by having eyelids, external ears, and less kinematic skulls.

Glossary

amniote
 animal that produces a terrestrially adapted egg protected by amniotic membranes

allantois
    membrane of the egg that stores nitrogenous wastes produced by the
    embryo; also facilitates respiration

amnion
    membrane of the egg that protects the embryo from mechanical shock
    and prevents dehydration

anapsid
    animal having no temporal fenestrae in the cranium

archosaur
    modern crocodilian or bird, or an extinct pterosaur or dinosaur

brumation
    period of much reduced metabolism and torpor that occurs in any
    ectotherm in cold weather

Casineria
    one of the oldest known amniotes; had both amphibian and reptilian
    characteristics

chorion
    membrane of the egg that surrounds the embryo and yolk sac

Crocodilia
    crocodiles and alligators

diapsid
    animal having two temporal fenestrae in the cranium

Hylonomus
    one of the earliest reptiles

lepidosaur
    modern lizards, snakes, and tuataras

sauropsid
    reptile or bird

Sphenodontia
    clade of tuataras

Squamata
    clade of lizards and snakes

synapsid
    mammal having one temporal fenestra

temporal fenestra
    non-orbital opening in the skull that may allow muscles to expand and
    lengthen

Testudines
    order of turtles

Birds
By the end of this section, you will be able to:

- Describe the evolutionary history of birds
- Describe the derived characteristics in birds that facilitate flight

The most obvious characteristic that sets birds apart from other modern vertebrates is the presence of feathers, which are modified scales. While vertebrates like bats fly without feathers, birds rely on feathers and wings, along with other modifications of body structure and physiology, for flight.

Characteristics of Birds

Birds are endothermic, and because they fly, they require large amounts of energy, necessitating a high metabolic rate. Like mammals, which are also endothermic, birds have an insulating covering that keeps heat in the body: feathers. Specialized feathers called **down feathers** are especially insulating, trapping air in spaces between each feather to decrease the rate of heat loss. Certain parts of a bird's body are covered in down feathers, and the base of other feathers have a downy portion, whereas newly hatched birds are covered in down.

Feathers not only act as insulation but also allow for flight, enabling the lift and thrust necessary to become airborne. The feathers on a wing are flexible, so the collective feathers move and separate as air moves through them, reducing the drag on the wing. **Flight feathers** are asymmetrical, which affects airflow over them and provides some of the lifting and thrusting force required for flight ([link]). Two types of flight feathers are found on the wings, primary feathers and secondary feathers. **Primary feathers** are located at the tip of the wing and provide thrust. **Secondary feathers** are located closer to the body, attach to the forearm portion of the wing and provide lift. **Contour feathers** are the feathers found on the body, and they help reduce drag produced by wind resistance during flight. They create a smooth, aerodynamic surface so that air moves smoothly over the bird's body, allowing for efficient flight.
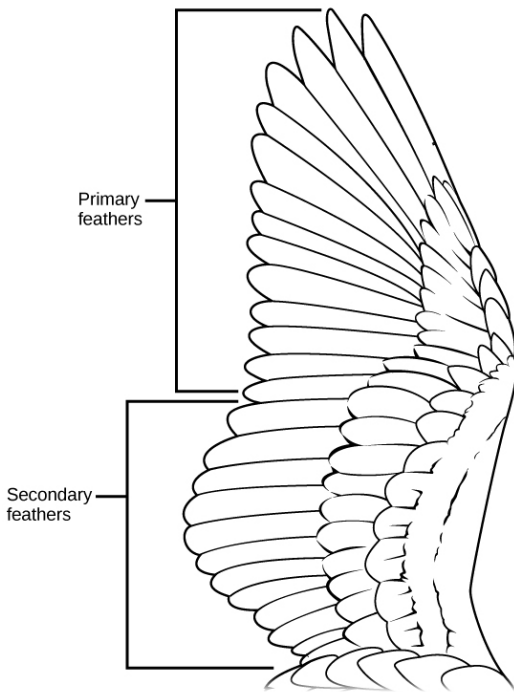
Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift.

Flapping of the entire wing occurs primarily through the actions of the chest muscles, the pectoralis and the supracoracoideus. These muscles are highly developed in birds and account for a higher percentage of body mass than in most mammals. These attach to a blade-shaped keel, like that of a boat, located on the sternum. The sternum of birds is larger than that of other vertebrates, which accommodates the large muscles required to generate enough upward force to generate lift with the flapping of the wings. Another skeletal modification found in most birds is the fusion of the two clavicles (collarbones), forming the **furcula** or wishbone. The furcula is flexible enough to bend and provide support to the shoulder girdle during flapping.

An important requirement of flight is a low body weight. As body weight increases, the muscle output required for flying increases. The largest living bird is the ostrich, and while it is much smaller than the largest mammals, it is flightless. For birds that do fly, reduction in body weight makes flight easier. Several modifications are found in birds to reduce body weight, including pneumatization of bones. **Pneumatic bones** are bones that are hollow, rather than filled with tissue ([link]). They contain air spaces that are sometimes connected to air sacs, and they have struts of bone to provide structural reinforcement. Pneumatic bones are not found in all birds, and they are more extensive in large birds than in small birds. Not all bones of the skeleton are pneumatic, although the skulls of almost all birds are.
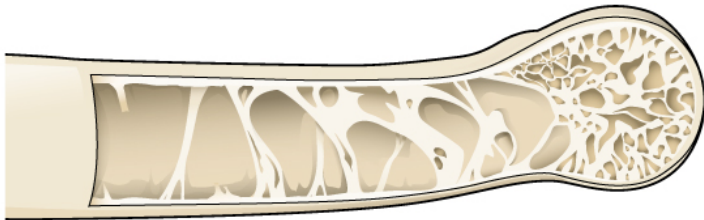
Many birds have hollow, pneumatic bones, which make flight easier.

Other modifications that reduce weight include the lack of a urinary bladder. Birds possess a cloaca, a structure that allows water to be reabsorbed from waste back into the bloodstream. Uric acid is not expelled as a liquid but is concentrated into urate salts, which are expelled along with fecal matter. In this way, water is not held in the urinary bladder, which would increase body weight. Most bird species only possess one ovary rather than two, further reducing body mass.

The air sacs that extend into bones to form pneumatic bones also join with the lungs and function in respiration. Unlike mammalian lungs in which air flows in two directions, as it is breathed in and out, airflow through bird lungs travels in one direction ([link]). Air sacs allow for this unidirectional

airflow, which also creates a cross-current exchange system with the blood. In a cross-current or counter-current system, the air flows in one direction and the blood flows in the opposite direction, creating a very efficient means of gas exchange.
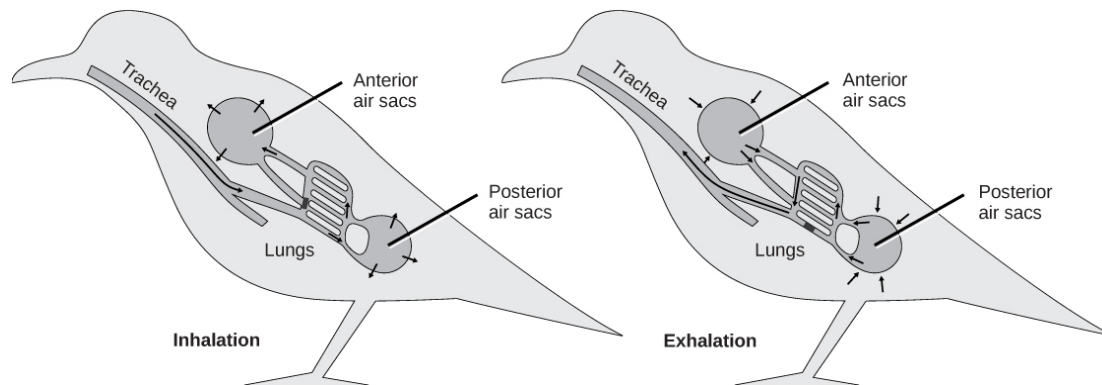
Avian respiration is an efficient system of gas exchange with air flowing unidirectionally. During inhalation, air passes from the trachea into posterior air sacs, then through the lungs to anterior air sacs. The air sacs are connected to the hollow interior of bones. During exhalation, air from air sacs passes into the lungs and out the trachea. (credit: modification of work by L. Shyamal)

Evolution of Birds

The evolutionary history of birds is still somewhat unclear. Due to the fragility of bird bones, they do not fossilize as well as other vertebrates. Birds are diapsids, meaning they have two fenestrations or openings in their skulls. Birds belong to a group of diapsids called the archosaurs, which also includes crocodiles and dinosaurs. It is commonly accepted that birds evolved from dinosaurs.

Dinosaurs (including birds) are further subdivided into two groups, the Saurischia ("lizard like") and the Ornithischia ("bird like"). Despite the

names of these groups, it was not the bird-like dinosaurs that gave rise to modern birds. Rather, Saurischia diverged into two groups: One included the long-necked herbivorous dinosaurs, such as Apatosaurus. The second group, bipedal predators called **theropods**, includes birds. This course of evolution is suggested by similarities between theropod fossils and birds, specifically in the structure of the hip and wrist bones, as well as the presence of the wishbone, formed by the fusing of the clavicles.

One important fossil of an animal intermediate to dinosaurs and birds is *Archaeopteryx*, which is from the Jurassic period ([link]). *Archaeopteryx* is important in establishing the relationship between birds and dinosaurs, because it is an intermediate fossil, meaning it has characteristics of both dinosaurs and birds. Some scientists propose classifying it as a bird, but others prefer to classify it as a dinosaur. The fossilized skeleton of *Archaeopteryx* looks like that of a dinosaur, and it had teeth whereas birds do not, but it also had feathers modified for flight, a trait associated only with birds among modern animals. Fossils of older feathered dinosaurs exist, but the feathers do not have the characteristics of flight feathers.

(a) *Archaeopteryx* lived in the late Jurassic Period around 150 million years ago. It had teeth like a dinosaur, but had (b) flight feathers like modern birds, which can be seen in this fossil.

It is still unclear exactly how flight evolved in birds. Two main theories exist, the arboreal ("tree") hypothesis and the terrestrial ("land") hypothesis. The arboreal hypothesis posits that tree-dwelling precursors to modern birds jumped from branch to branch using their feathers for gliding before becoming fully capable of flapping flight. In contrast to this, the terrestrial hypothesis holds that running was the stimulus for flight, as wings could be used to improve running and then became used for flapping flight. Like the question of how flight evolved, the question of how endothermy evolved in birds still is unanswered. Feathers provide insulation, but this is only beneficial if body heat is being produced internally. Similarly, internal heat production is only viable if insulation is present to retain that heat. It has been suggested that one or the other—feathers or endothermy—evolved in response to some other selective pressure.

During the Cretaceous period, a group known as the **Enantiornithes** was the dominant bird type ([link]). Enantiornithes means "opposite birds," which refers to the fact that certain bones of the feet are joined differently than the way the bones are joined in modern birds. These birds formed an evolutionary line separate from modern birds, and they did not survive past the Cretaceous. Along with the Enantiornithes, Ornithurae birds (the evolutionary line that includes modern birds) were also present in the Cretaceous. After the extinction of Enantiornithes, modern birds became the dominant bird, with a large radiation occurring during the Cenozoic Era. Referred to as **Neornithes** ("new birds"), modern birds are now classified into two groups, the **Paleognathae** ("old jaw") or ratites, a group of flightless birds including ostriches, emus, rheas, and kiwis, and the **Neognathae** ("new jaw"), which includes all other birds.

Shanweiniao cooperorum was a species of Enantiornithes that did not survive past the Cretaceous period. (credit: Nobu Tamura)

Note:
Career Connection
Veterinarian
Veterinarians treat diseases, disorders, and injuries in animals, primarily vertebrates. They treat pets, livestock, and animals in zoos and laboratories. Veterinarians usually treat dogs and cats, but also treat birds, reptiles, rabbits, and other animals that are kept as pets. Veterinarians that work with farms and ranches treat pigs, goats, cows, sheep, and horses. Veterinarians are required to complete a degree in veterinary medicine, which includes taking courses in animal physiology, anatomy, microbiology, and pathology, among many other courses. The physiology and biochemistry of different vertebrate species differ greatly. Veterinarians are also trained to perform surgery on many different vertebrate species, which requires an understanding of the vastly different anatomies of various species. For example, the stomach of ruminants like cows has four compartments versus one compartment for non-ruminants. Birds also have unique anatomical adaptations that allow for flight.

Some veterinarians conduct research in academic settings, broadening our knowledge of animals and medical science. One area of research involves understanding the transmission of animal diseases to humans, called zoonotic diseases. For example, one area of great concern is the transmission of the avian flu virus to humans. One type of avian flu virus, H5N1, is a highly pathogenic strain that has been spreading in birds in Asia, Europe, Africa, and the Middle East. Although the virus does not cross over easily to humans, there have been cases of bird-to-human transmission. More research is needed to understand how this virus can cross the species barrier and how its spread can be prevented.

Section Summary

Birds are endothermic, meaning they produce their own body heat and regulate their internal temperature independently of the external temperature. Feathers not only act as insulation but also allow for flight, providing lift with secondary feathers and thrust with primary feathers. Pneumatic bones are bones that are hollow rather than filled with tissue, containing air spaces that are sometimes connected to air sacs. Airflow through bird lungs travels in one direction, creating a cross-current exchange with the blood. Birds are diapsids and belong to a group called the archosaurs. Birds are thought to have evolved from theropod dinosaurs. The oldest known fossil of a bird is that of *Archaeopteryx*, which is from the Jurassic period. Modern birds are now classified into two groups, Paleognathae and Neognathae.

Review Questions

Exercise:

Problem: A bird or feathered dinosaur is _____.

    a. Neornithes
    b. *Archaeopteryx*
    c. Enantiornithes

d. Paleognathae

Solution:

B

Exercise:

Problem:

Which of the following feather types helps to reduce drag produced by wind resistance during flight?

a. flight feathers
b. primary feathers
c. secondary feathers
d. contour feathers

Solution:

D

Free Response

Exercise:

Problem:

Explain why birds are thought to have evolved from theropod dinosaurs.

Solution:

This is suggested by similarities observed between theropod fossils and birds, specifically in the design of the hip and wrist bones, as well as the presence of a furcula, or wishbone, formed by the fusing of the clavicles.

Exercise:

Problem:

Describe three skeletal adaptations that allow for flight in birds.

Solution:

The sternum of birds is larger than that of other vertebrates, which accommodates the force required for flapping. Another skeletal modification is the fusion of the clavicles, forming the furcula or wishbone. The furcula is flexible enough to bend during flapping and provides support to the shoulder girdle during flapping. Birds also have pneumatic bones that are hollow rather than filled with tissue.

Glossary

Archaeopteryx
> transition species from dinosaur to bird from the Jurassic period

contour feather
> feather that creates an aerodynamic surface for efficient flight

down feather
> feather specialized for insulation

Enantiornithes
> dominant bird group during the Cretaceous period

flight feather
> feather specialized for flight

furcula
> wishbone formed by the fusing of the clavicles

Neognathae
> birds other than the Paleognathae

Neornithes
    modern birds

Paleognathae
    ratites; flightless birds, including ostriches and emus

pneumatic bone
    air-filled bone

primary feather
    feather located at the tip of the wing that provides thrust

secondary feather
    feather located at the base of the wing that provides lift

theropod
    dinosaur group ancestral to birds

Mammals
By the end of this section, you will be able to:

- Name and describe the distinguishing features of the three main groups of mammals
- Describe the proposed line of descent that produced mammals
- List some derived features that may have arisen in response to mammals' need for constant, high-level metabolism

Mammals are vertebrates that possess hair and mammary glands. Several other characteristics are distinctive to mammals, including certain features of the jaw, skeleton, integument, and internal anatomy. Modern mammals belong to three clades: monotremes, marsupials, and eutherians (or placental mammals).

Characteristics of Mammals

The presence of hair is one of the most obvious signs of a mammal. Although it is not very extensive on certain species, such as whales, hair has many important functions for mammals. Mammals are endothermic, and hair provides insulation to retain heat generated by metabolic work. Hair traps a layer of air close to the body, retaining heat. Along with insulation, hair can serve as a sensory mechanism via specialized hairs called vibrissae, better known as whiskers. These attach to nerves that transmit information about sensation, which is particularly useful to nocturnal or burrowing mammals. Hair can also provide protective coloration or be part of social signaling, such as when an animal's hair stands "on end."

Mammalian integument, or skin, includes secretory glands with various functions. **Sebaceous glands** produce a lipid mixture called sebum that is secreted onto the hair and skin for water resistance and lubrication. Sebaceous glands are located over most of the body. **Eccrine glands** produce sweat, or perspiration, which is mainly composed of water. In most mammals, eccrine glands are limited to certain areas of the body, and some mammals do not possess them at all. However, in primates, especially humans, sweat figures prominently in thermoregulation, regulating the body through evaporative cooling. Sweat glands are located over most of the

body surface in primates. **Apocrine glands**, or scent glands, secrete substances that are used for chemical communication, such as in skunks. **Mammary glands** produce milk that is used to feed newborns. While male monotremes and eutherians possess mammary glands, male marsupials do not. Mammary glands likely are modified sebaceous or eccrine glands, but their evolutionary origin is not entirely clear.

The skeletal system of mammals possesses many unique features. The lower jaw of mammals consists of only one bone, the **dentary**. The jaws of other vertebrates are composed of more than one bone. In mammals, the dentary bone joins the skull at the squamosal bone, while in other vertebrates, the quadrate bone of the jaw joins with the articular bone of the skull. These bones are present in mammals, but they have been modified to function in hearing and form bones in the middle ear ([link]). Other vertebrates possess only one middle ear bone, the stapes. Mammals have three: the malleus, incus, and stapes. The malleus originated from the articular bone, whereas the incus originated from the quadrate bone. This arrangement of jaw and ear bones aids in distinguishing fossil mammals from fossils of other synapsids.
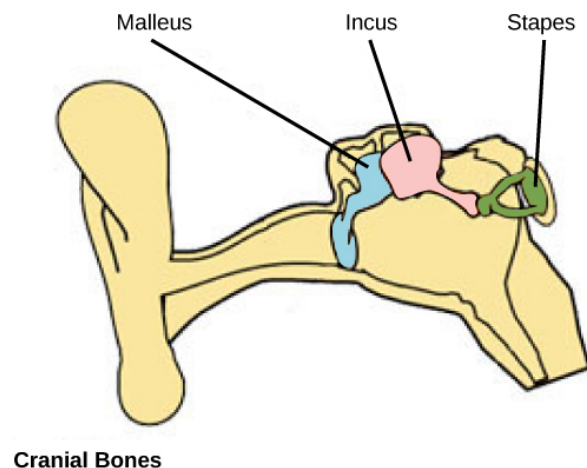
Cranial Bones

Bones of the mammalian inner ear are modified from bones of the jaw and skull. (credit: NCI)

The adductor muscle that closes the jaw is composed of two muscles in mammals: the temporalis and the masseter. These allow side-to-side movement of the jaw, making chewing possible, which is unique to mammals. Most mammals have **heterodont teeth**, meaning that they have different types and shapes of teeth rather than just one type and shape of tooth. Most mammals are **diphyodonts**, meaning that they have two sets of teeth in their lifetime: deciduous or "baby" teeth, and permanent teeth. Other vertebrates are polyphyodonts, that is, their teeth are replaced throughout their entire life.

Mammals, like birds, possess a four-chambered heart. Mammals also have a specialized group of cardiac fibers located in the walls of their right atrium called the sinoatrial node, or pacemaker, which determines the rate at which the heart beats. Mammalian erythrocytes (red blood cells) do not have nuclei, whereas the erythrocytes of other vertebrates are nucleated.

The kidneys of mammals have a portion of the nephron called the loop of Henle or nephritic loop, which allows mammals to produce urine with a high concentration of solutes, higher than that of the blood. Mammals lack a renal portal system, which is a system of veins that moves blood from the hind or lower limbs and region of the tail to the kidneys. Renal portal systems are present in all other vertebrates except jawless fishes. A urinary bladder is present in all mammals.

Mammalian brains have certain characteristics that differ from other vertebrates. In some, but not all mammals, the cerebral cortex, the outermost part of the cerebrum, is highly folded, allowing for a greater surface area than is possible with a smooth cortex. The optic lobes, located in the midbrain, are divided into two parts in mammals, whereas other vertebrates possess a single, undivided lobe. Eutherian mammals also possess a specialized structure that links the two cerebral hemispheres, called the corpus callosum.

Evolution of Mammals

Mammals are synapsids, meaning they have a single opening in the skull. They are the only living synapsids, as earlier forms became extinct by the Jurassic period. The early non-mammalian synapsids can be divided into two groups, the pelycosaurs and the therapsids. Within the therapsids, a group called the cynodonts are thought to be the ancestors of mammals ([link]).

Cynodonts, which first appeared in the Late Permian period 260 million years ago, are thought to be the ancestors of modern mammals. (credit: Nobu Tamura)

A key characteristic of synapsids is endothermy, rather than the ectothermy seen in most other vertebrates. The increased metabolic rate required to internally modify body temperature went hand in hand with changes to certain skeletal structures. The later synapsids, which had more evolved characteristics unique to mammals, possess cheeks for holding food and heterodont teeth, which are specialized for chewing, mechanically breaking down food to speed digestion and releasing the energy needed to produce heat. Chewing also requires the ability to chew and breathe at the same time, which is facilitated by the presence of a secondary palate. A secondary palate separates the area of the mouth where chewing occurs from the area above where respiration occurs, allowing breathing to proceed uninterrupted during chewing. A secondary palate is not found in

pelycosaurs but is present in cynodonts and mammals. The jawbone also shows changes from early synapsids to later ones. The zygomatic arch, or cheekbone, is present in mammals and advanced therapsids such as cynodonts, but is not present in pelycosaurs. The presence of the zygomatic arch suggests the presence of the masseter muscle, which closes the jaw and functions in chewing.

In the appendicular skeleton, the shoulder girdle of therian mammals is modified from that of other vertebrates in that it does not possess a procoracoid bone or an interclavicle, and the scapula is the dominant bone.

Mammals evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period, some 205 million years ago. Early mammals were small, about the size of a small rodent. Mammals first began to diversify in the Mesozoic Era, from the Jurassic to the Cretaceous periods, although most of these mammals were extinct by the end of the Mesozoic. During the Cretaceous period, another radiation of mammals began and continued through the Cenozoic Era, about 65 million years ago.

Living Mammals

The eutherians, or placental mammals, and the marsupials together comprise the clade of therian mammals. Monotremes, or metatherians, form their sister clade.

There are three living species of **monotremes**: the platypus and two species of echidnas, or spiny anteaters. The leathery-beaked platypus belongs to the family **Ornithorhynchidae** ("bird beak"), whereas echidnas belong to the family **Tachyglossidae** ("sticky tongue") ([link]). The platypus and one species of echidna are found in Australia, and the other species of echidna is found in New Guinea. Monotremes are unique among mammals as they lay eggs, rather than giving birth to live young. The shells of their eggs are not like the hard shells of birds, but are a leathery shell, similar to the shells of reptile eggs. Monotremes have no teeth.

(a) The platypus, a monotreme, possesses a leathery beak and lays eggs rather than giving birth to live young. (b) The echidna is another monotreme. (credit b: modification of work by Barry Thomas)

Marsupials are found primarily in Australia, though the opossum is found in North America. Australian marsupials include the kangaroo, koala, bandicoot, Tasmanian devil ([link]), and several other species. Most species of marsupials possess a pouch in which the very premature young reside after birth, receiving milk and continuing to develop. Marsupials differ from eutherians in that there is a less complex placental connection: The young are born at an extremely early age and latch onto the nipple within the pouch.

The Tasmanian devil is one of

several marsupials native to Australia. (credit: Wayne McLean)

Eutherians are the most widespread of the mammals, occurring throughout the world. There are 18 to 20 orders of placental mammals. Some examples are Insectivora, the insect eaters; Edentata, the toothless anteaters; Rodentia, the rodents; Cetacea, the aquatic mammals including whales; Carnivora, carnivorous mammals including dogs, cats, and bears; and Primates, which includes humans. **Eutherian mammals** are sometimes called placental mammals because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. While other mammals possess a less complex placenta or briefly have a placenta, all eutherians possess a complex placenta during gestation.

Section Summary

Mammals in general are vertebrates that possess hair and mammary glands. The mammalian integument includes various secretory glands, including sebaceous glands, eccrine glands, apocrine glands, and mammary glands. Mammals are synapsids, meaning that they have a single opening in the skull. A key characteristic of synapsids is endothermy rather than the ectothermy seen in other vertebrates. Mammals probably evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period. There are three groups of mammals living today: monotremes, marsupials, and eutherians. Monotremes are unique among mammals as they lay eggs, rather than giving birth to young. Eutherian mammals are sometimes called placental mammals, because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange.

Review Questions

Exercise:

Problem: Eccrine glands produce _____.

    a. sweat
    b. lipids
    c. scents
    d. milk

Solution:

A

Exercise:

Problem: Monotremes include:

    a. kangaroos
    b. koalas
    c. bandicoots
    d. platypuses

Solution:

D

Free Response

Exercise:

Problem:

Describe three unique features of the mammalian skeletal system.

Solution:

The lower jaw of mammals consists of only one bone, the dentary. The dentary bone joins the skull at the squamosal bone. Mammals have three bones of the middle ear. The adductor muscle that closes the jaw is composed of two muscles in mammals. Most mammals have heterodont teeth.

Exercise:

Problem:

Describe three characteristics of the mammalian brain that differ from other vertebrates.

Solution:

In some mammals, the cerebral cortex is highly folded, allowing for greater surface area than a smooth cortex. The optic lobes are divided into two parts in mammals. Eutherian mammals also possess a specialized structure that links the two cerebral hemispheres, called the corpus callosum.

Glossary

apocrine gland
 scent gland that secretes substances that are used for chemical communication

dentary
 single bone that comprises the lower jaw of mammals

diphyodont
 refers to the possession of two sets of teeth in a lifetime

eccrine gland
 sweat gland

eutherian mammal

mammal that possesses a complex placenta, which connects a fetus to the mother; sometimes called placental mammals

heterodont tooth
different types of teeth that are modified for different purposes

mammal
one of the groups of endothermic vertebrates that possesses hair and mammary glands

mammary gland
in female mammals, a gland that produces milk for newborns

marsupial
one of the groups of mammals that includes the kangaroo, koala, bandicoot, Tasmanian devil, and several other species; young develop within a pouch

monotreme
egg-laying mammal

Ornithorhynchidae
clade that includes the duck-billed platypus

sebaceous gland
in mammals, a skin gland that produce a lipid mixture called *sebum*

Tachyglossidae
clade that includes the echidna or spiny anteater

Introduction
class="introduction"

An arctic fox is a complex animal, well adapted to its environment. It changes coat color with the seasons, and has longer fur in winter to trap heat. (credit: modification of work by Keith Morehouse, USFWS)

The arctic fox is an example of a complex animal that has adapted to its environment and illustrates the relationships between an animal's form and function. The structures of animals consist of primary tissues that make up more complex organs and organ systems. Homeostasis allows an animal to maintain a balance between its internal and external environments.

Animal Primary Tissues
By the end of this section, you will be able to:

- Describe epithelial tissues
- Discuss the different types of connective tissues in animals
- Describe three types of muscle tissues
- Describe nervous tissue

The tissues of multicellular, complex animals are four primary types: epithelial, connective, muscle, and nervous. Recall that tissues are groups of similar cells group of similar cells carrying out related functions. These tissues combine to form organs—like the skin or kidney—that have specific, specialized functions within the body. Organs are organized into organ systems to perform functions; examples include the circulatory system, which consists of the heart and blood vessels, and the digestive system, consisting of several organs, including the stomach, intestines, liver, and pancreas. Organ systems come together to create an entire organism.

Epithelial Tissues

Epithelial tissues cover the outside of organs and structures in the body and line the lumens of organs in a single layer or multiple layers of cells. The types of epithelia are classified by the shapes of cells present and the number of layers of cells. Epithelia composed of a single layer of cells is called **simple epithelia**; epithelial tissue composed of multiple layers is called **stratified epithelia**. [link] summarizes the different types of epithelial tissues.

Different Types of Epithelial Tissues		
Cell shape	**Description**	**Location**

Different Types of Epithelial Tissues

Cell shape	Description	Location
squamous	flat, irregular round shape	simple: lung alveoli, capillaries stratified: skin, mouth, vagina
cuboidal	cube shaped, central nucleus	glands, renal tubules
columnar	tall, narrow, nucleus toward base tall, narrow, nucleus along cell	simple: digestive tract pseudostratified: respiratory tract
transitional	round, simple but appear stratified	urinary bladder

Squamous Epithelia

Squamous epithelial cells are generally round, flat, and have a small, centrally located nucleus. The cell outline is slightly irregular, and cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs and the exchange of nutrients and waste at blood capillaries.
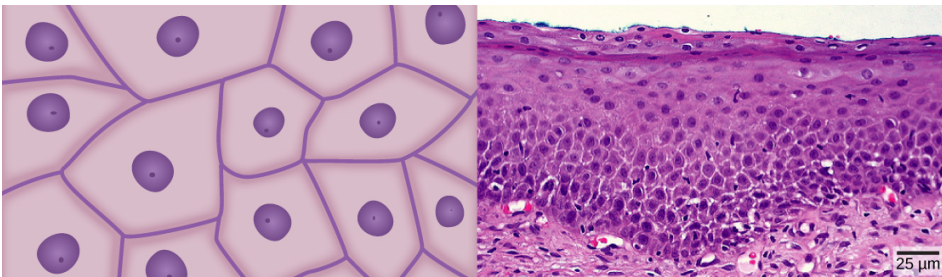
Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell)

[link]**a** illustrates a layer of squamous cells with their membranes joined together to form an epithelium. Image [link]**b** illustrates squamous epithelial cells arranged in stratified layers, where protection is needed on the body from outside abrasion and damage. This is called a stratified squamous epithelium and occurs in the skin and in tissues lining the mouth and vagina.

Cuboidal Epithelia

Cuboidal epithelial cells, shown in [link], are cube-shaped with a single, central nucleus. They are most commonly found in a single layer representing a simple epithelia in glandular tissues throughout the body where they prepare and secrete glandular material. They are also found in the walls of tubules and in the ducts of the kidney and liver.
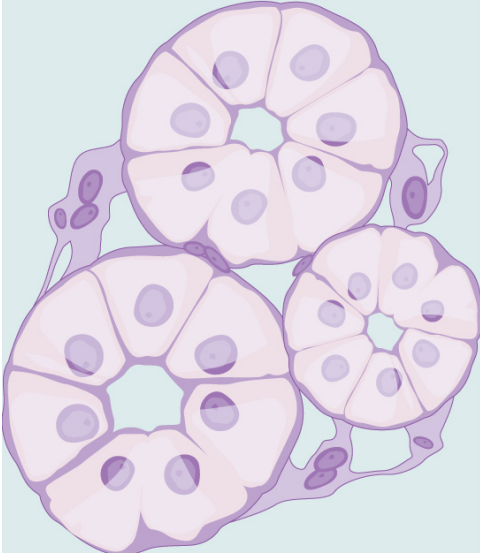
Simple cuboidal epithelial cells line tubules in the mammalian kidney, where they are involved in filtering the blood.

Columnar Epithelia

Columnar epithelial cells are taller than they are wide: they resemble a stack of columns in an epithelial layer, and are most commonly found in a single-layer arrangement. The nuclei of columnar epithelial cells in the digestive tract appear to be lined up at the base of the cells, as illustrated in [link]. These cells absorb material from the lumen of the digestive tract and prepare it for entry into the body through the circulatory and lymphatic systems.
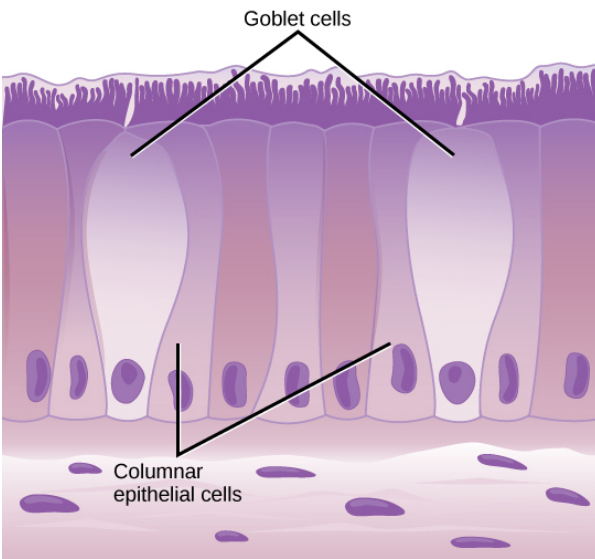
Simple columnar epithelial cells absorb material from the digestive tract. Goblet cells secret mucous into the digestive tract lumen.

Columnar epithelial cells lining the respiratory tract appear to be stratified. However, each cell is attached to the base membrane of the tissue and, therefore, they are simple tissues. The nuclei are arranged at different levels in the layer of cells, making it appear as though there is more than one layer, as seen in [link]. This is called **pseudostratified**, columnar epithelia. This cellular covering has cilia at the apical, or free, surface of the cells. The cilia enhance the movement of mucous and trapped particles out of the respiratory tract, helping to protect the system from invasive microorganisms and harmful material that has been breathed into the body. Goblet cells are interspersed in some tissues (such as the lining of the trachea). The goblet cells contain mucous that traps irritants, which in the case of the trachea keep these irritants from getting into the lungs.
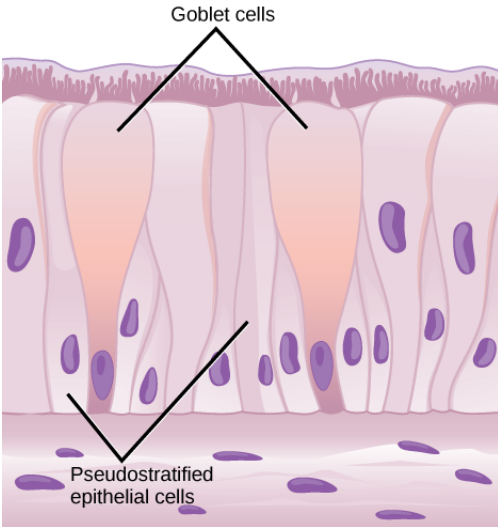
Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucous into the respiratory tract.

Transitional Epithelia

Transitional or uroepithelial cells appear only in the urinary system, primarily in the bladder and ureter. These cells are arranged in a stratified layer, but they have the capability of appearing to pile up on top of each other in a relaxed, empty bladder, as illustrated in [link]. As the urinary bladder fills, the epithelial layer unfolds and expands to hold the volume of

urine introduced into it. As the bladder fills, it expands and the lining becomes thinner. In other words, the tissue transitions from thick to thin.
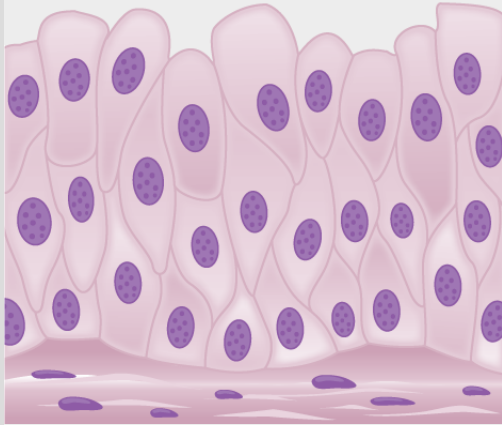
Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is.

Which of the following statements about types of epithelial cells is false?

a. Simple columnar epithelial cells line the tissue of the lung.
b. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
c. Pseudostratisfied columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
d. Transitional epithelia change in thickness depending on how full the bladder is.

Connective Tissues

Connective tissues are made up of a matrix consisting of living cells and a non-living substance, called the ground substance. The ground substance is made of an organic substance (usually a protein) and an inorganic substance (usually a mineral or water). The principal cell of connective tissues is the fibroblast. This cell makes the fibers found in nearly all of the connective tissues. Fibroblasts are motile, able to carry out mitosis, and can synthesize whichever connective tissue is needed. Macrophages, lymphocytes, and, occasionally, leukocytes can be found in some of the tissues. Some tissues have specialized cells that are not found in the others. The **matrix** in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has proportionally a less dense matrix.

The organic portion or protein fibers found in connective tissues are either collagen, elastic, or reticular fibers. Collagen fibers provide strength to the tissue, preventing it from being torn or separated from the surrounding tissues. Elastic fibers are made of the protein elastin; this fiber can stretch to one and one half of its length and return to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers are the third type of protein fiber found in connective tissues. This fiber consists of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected. The various types of connective tissues, the types of cells and fibers they are made of, and sample locations of the tissues is summarized in [link].

Connective Tissues			
Tissue	**Cells**	**Fibers**	**Location**

Connective Tissues

Tissue	Cells	Fibers	Location
loose/areolar	fibroblasts, macrophages, some lymphocytes, some neutrophils	few: collagen, elastic, reticular	around blood vessels; anchors epithelia
dense, fibrous connective tissue	fibroblasts, macrophages,	mostly collagen	irregular: skin regular: tendons, ligaments
cartilage	chondrocytes, chondroblasts	hyaline: few collagen fibrocartilage: large amount of collagen	shark skeleton, fetal bones, human ears, intervertebral discs
bone	osteoblasts, osteocytes, osteoclasts	some: collagen, elastic	vertebrate skeletons
adipose	adipocytes	few	adipose (fat)
blood	red blood cells, white blood cells	none	blood

Loose/Areolar Connective Tissue

Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. As illustrated in [link], loose connective tissue has some fibroblasts; macrophages are present as well. Collagen fibers are relatively wide and stain a light pink, while elastic fibers are thin and stain dark blue to black. The space between the formed elements of the tissue is filled with the matrix. The material in the connective tissue gives it a loose consistency similar to a cotton ball that has been pulled apart. Loose connective tissue is found around every blood vessel and helps to keep the vessel in place. The tissue is also found around and between most body organs. In summary, areolar tissue is tough, yet flexible, and comprises membranes.
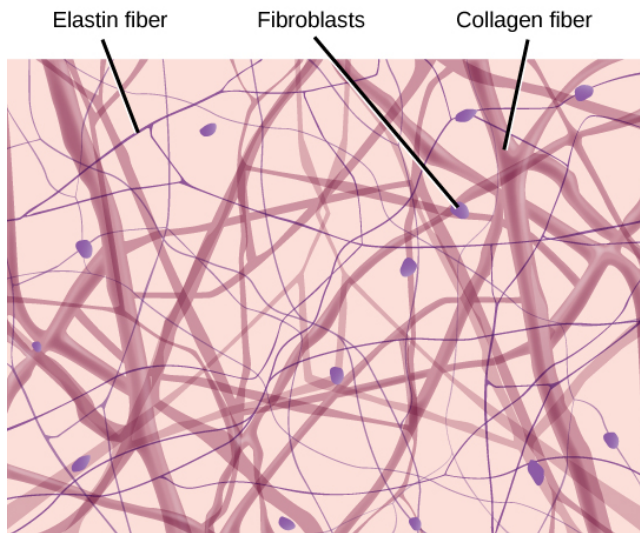
Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts.

Fibrous Connective Tissue

Fibrous connective tissues contain large amounts of collagen fibers and few cells or matrix material. The fibers can be arranged irregularly or regularly with the strands lined up in parallel. Irregularly arranged fibrous connective tissues are found in areas of the body where stress occurs from all directions, such as the dermis of the skin. Regular fibrous connective tissue, shown in [link], is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).
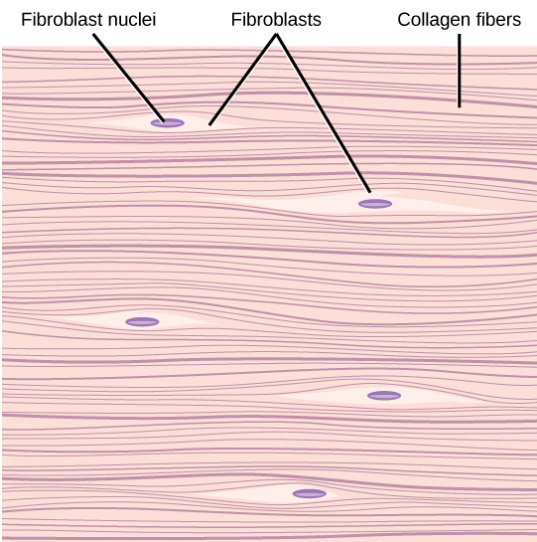
Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel.

Cartilage

Cartilage is a connective tissue with a large amount of the matrix and variable amounts of fibers. The cells, called **chondrocytes**, make the matrix

and fibers of the tissue. Chondrocytes are found in spaces within the tissue called **lacunae**.

A cartilage with few collagen and elastic fibers is hyaline cartilage, illustrated in [link]. The lacunae are randomly scattered throughout the tissue and the matrix takes on a milky or scrubbed appearance with routine histological stains. Sharks have cartilaginous skeletons, as does nearly the entire human skeleton during a specific pre-birth developmental stage. A remnant of this cartilage persists in the outer portion of the human nose. Hyaline cartilage is also found at the ends of long bones, reducing friction and cushioning the articulations of these bones.
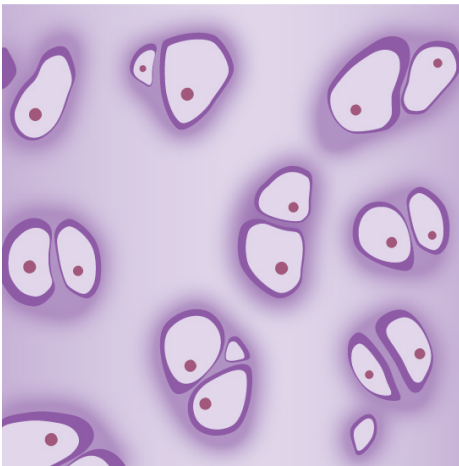
Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae.

Elastic cartilage has a large amount of elastic fibers, giving it tremendous flexibility. The ears of most vertebrate animals contain this cartilage as do portions of the larynx, or voice box. Fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage comprises the intervertebral discs in vertebrate animals. Hyaline cartilage found in movable joints such as the knee and shoulder becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage and results in the joints becoming "stiff."

Bone

Bone, or osseous tissue, is a connective tissue that has a large amount of two different types of matrix material. The organic matrix is similar to the matrix material found in other connective tissues, including some amount of collagen and elastic fibers. This gives strength and flexibility to the tissue. The inorganic matrix consists of mineral salts—mostly calcium salts—that give the tissue hardness. Without adequate organic material in the matrix, the tissue breaks; without adequate inorganic material in the matrix, the tissue bends.

There are three types of cells in bone: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are active in making bone for growth and remodeling. Osteoblasts deposit bone material into the matrix and, after the matrix surrounds them, they continue to live, but in a reduced metabolic state as osteocytes. Osteocytes are found in lacunae of the bone. Osteoclasts are active in breaking down bone for bone remodeling, and they provide access to calcium stored in tissues. Osteoclasts are usually found on the surface of the tissue.

Bone can be divided into two types: compact and spongy. Compact bone is found in the shaft (or diaphysis) of a long bone and the surface of the flat bones, while spongy bone is found in the end (or epiphysis) of a long bone. Compact bone is organized into subunits called **osteons**, as illustrated in [link]. A blood vessel and a nerve are found in the center of the structure within the Haversian canal, with radiating circles of lacunae around it known as lamellae. The wavy lines seen between the lacunae are

microchannels called **canaliculi**; they connect the lacunae to aid diffusion between the cells. Spongy bone is made of tiny plates called **trabeculae** these plates serve as struts to give the spongy bone strength. Over time, these plates can break causing the bone to become less resilient. Bone tissue forms the internal skeleton of vertebrate animals, providing structure to the animal and points of attachment for tendons.

(a)

(b)

(c)
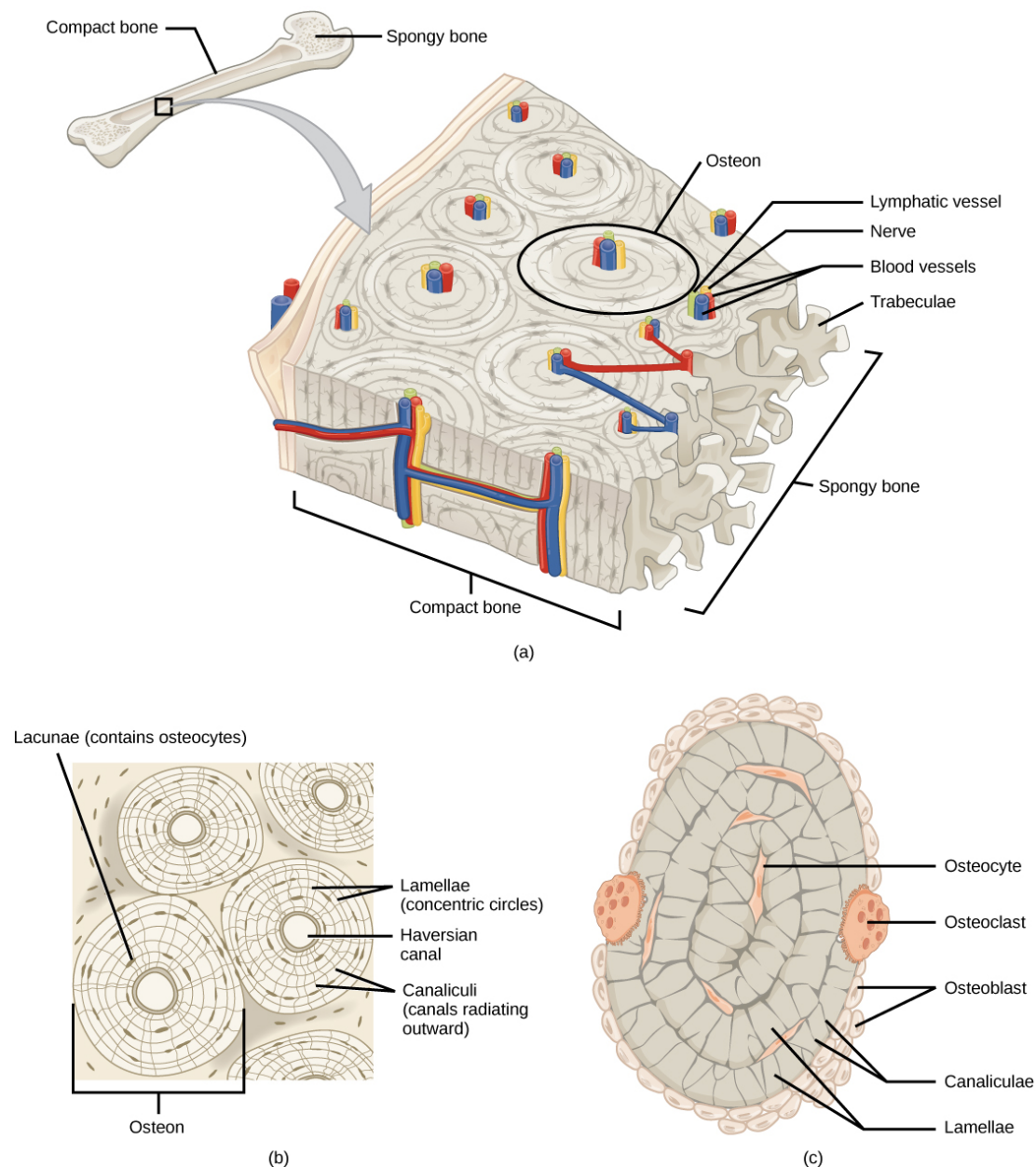
(a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are microchannels connecting the lacunae together. (c) Osteoblasts surround the exterior of the bone. Osteoclasts bore tunnels into the bone and osteocytes are found in the lacunae.

Adipose Tissue

Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix and only has a few fibers. Adipose tissue is made up of cells called adipocytes that collect and store fat in the form of triglycerides, for energy metabolism. Adipose tissues additionally serve as insulation to help maintain body temperatures, allowing animals to be endothermic, and they function as cushioning against damage to body organs. Under a microscope, adipose tissue cells appear empty due to the extraction of fat during the processing of the material for viewing, as seen in [link]. The thin lines in the image are the cell membranes, and the nuclei are the small, black dots at the edges of the cells.
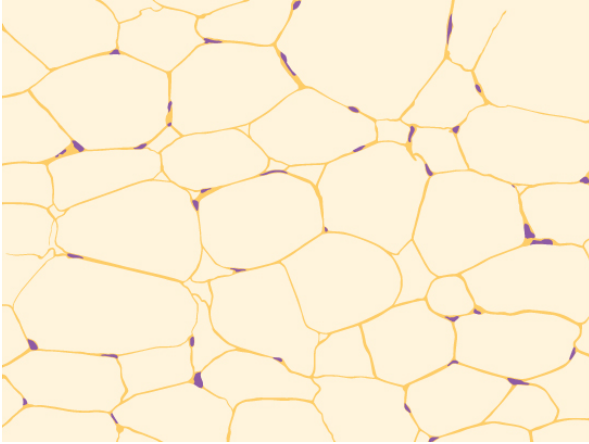
Adipose is a connective tissue is made up of cells called adipocytes. Adipocytes have small nuclei localized at the cell edge.

Blood

Blood is considered a connective tissue because it has a matrix, as shown in [link]. The living cell types are red blood cells (RBC), also called erythrocytes, and white blood cells (WBC), also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.
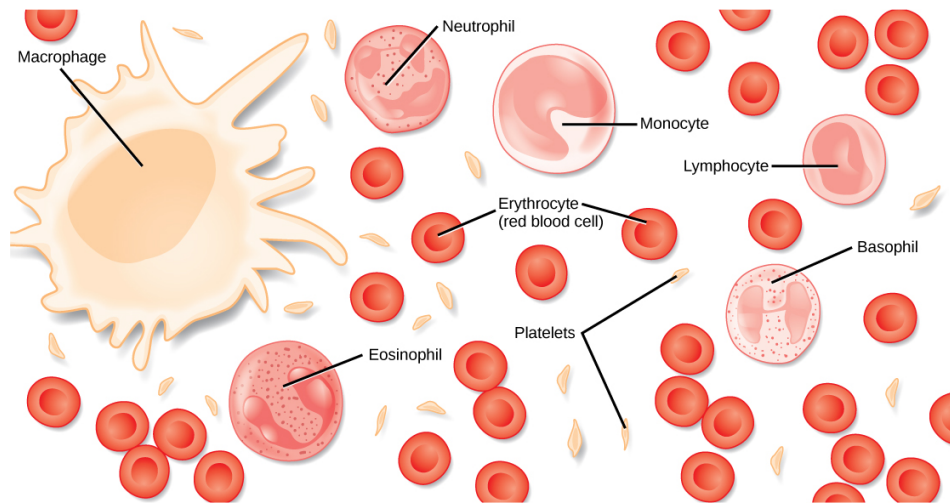
Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

The cell found in greatest abundance in blood is the erythrocyte. Erythrocytes are counted in millions in a blood sample: the average number of red blood cells in primates is 4.7 to 5.5 million cells per microliter. Erythrocytes are consistently the same size in a species, but vary in size between species. For example, the average diameter of a primate red blood cell is 7.5 µl, a dog is close at 7.0 µl, but a cat's RBC diameter is 5.9 µl. Sheep erythrocytes are even smaller at 4.6 µl. Mammalian erythrocytes lose their nuclei and mitochondria when they are released from the bone marrow where they are made. Fish, amphibian, and avian red blood cells maintain their nuclei and mitochondria throughout the cell's life. The principal job of an erythrocyte is to carry and deliver oxygen to the tissues.

Leukocytes are the predominant white blood cells found in the peripheral blood. Leukocytes are counted in the thousands in the blood with measurements expressed as ranges: primate counts range from 4,800 to 10,800 cells per µl, dogs from 5,600 to 19,200 cells per µl, cats from 8,000

to 25,000 cells per µl, cattle from 4,000 to 12,000 cells per µl, and pigs from 11,000 to 22,000 cells per µl.

Lymphocytes function primarily in the immune response to foreign antigens or material. Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells and they participate in one of the early lines of defense against microbial invaders, aiding in the removal of bacteria that has entered the body. Another leukocyte that is found in the peripheral blood is the monocyte. Monocytes give rise to phagocytic macrophages that clean up dead and damaged cells in the body, whether they are foreign or from the host animal. Two additional leukocytes in the blood are eosinophils and basophils—both help to facilitate the inflammatory response.

The slightly granular material among the cells is a cytoplasmic fragment of a cell in the bone marrow. This is called a platelet or thrombocyte. Platelets participate in the stages leading up to coagulation of the blood to stop bleeding through damaged blood vessels. Blood has a number of functions, but primarily it transports material through the body to bring nutrients to cells and remove waste material from them.

Muscle Tissues

There are three types of muscle in animal bodies: smooth, skeletal, and cardiac. They differ by the presence or absence of striations or bands, the number and location of nuclei, whether they are voluntarily or involuntarily controlled, and their location within the body. [link] summarizes these differences.

Types of Muscles

Types of Muscles of				
Muscle	Striations	Nuclei	Control	Location
Type of Muscle	Striations	Nuclei	Control	Location
smooth	no	single, in center	involuntary	visceral organs
skeletal	yes	many, at periphery	voluntary	skeletal muscles
cardiac	yes	single, in center	involuntary	heart

Smooth Muscle

Smooth muscle does not have striations in its cells. It has a single, centrally located nucleus, as shown in [link]. Constriction of smooth muscle occurs under involuntary, autonomic nervous control and in response to local conditions in the tissues. Smooth muscle tissue is also called non-striated as it lacks the banded appearance of skeletal and cardiac muscle. The walls of blood vessels, the tubes of the digestive system, and the tubes of the reproductive systems are composed of mostly smooth muscle.

Smooth muscle cells   Skeletal muscle cells   Cardiac muscle cells
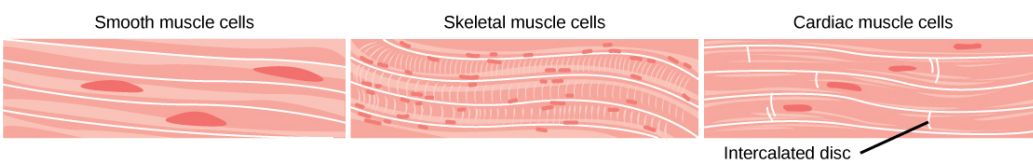
Intercalated disc

Smooth muscle cells do not have striations, while skeletal

muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

Skeletal Muscle

Skeletal muscle has striations across its cells caused by the arrangement of the contractile proteins actin and myosin. These muscle cells are relatively long and have multiple nuclei along the edge of the cell. Skeletal muscle is under voluntary, somatic nervous system control and is found in the muscles that move bones. [link] illustrates the histology of skeletal muscle.

Cardiac Muscle

Cardiac muscle, shown in [link], is found only in the heart. Like skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally located nucleus. Cardiac muscle is not under voluntary control but can be influenced by the autonomic nervous system to speed up or slow down. An added feature to cardiac muscle cells is a line than extends along the end of the cell as it abuts the next cardiac cell in the row. This line is called an intercalated disc: it assists in passing electrical impulse efficiently from one cell to the next and maintains the strong connection between neighboring cardiac cells.

Nervous Tissues

Nervous tissues are made of cells specialized to receive and transmit electrical impulses from specific areas of the body and to send them to specific locations in the body. The main cell of the nervous system is the

neuron, illustrated in [link]. The large structure with a central nucleus is the cell body of the neuron. Projections from the cell body are either dendrites specialized in receiving input or a single axon specialized in transmitting impulses. Some glial cells are also shown. Astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells that are not shown support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic and remove debris or damaged cells from the tissue. A nerve consists of neurons and glial cells.
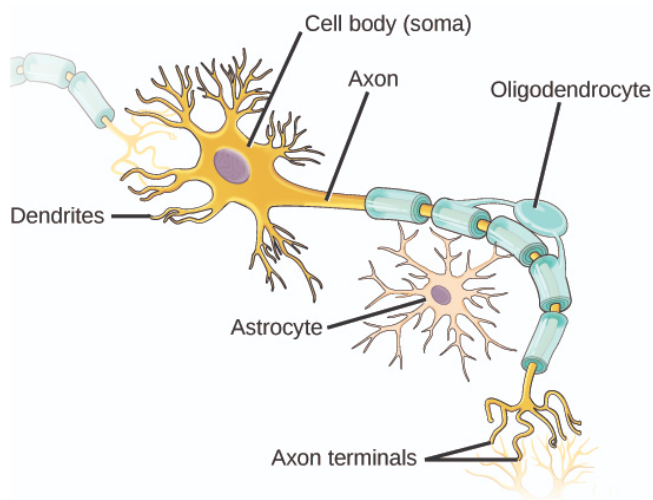
The neuron has projections called dendrites that receive signals and projections called axons that send signals. Also shown are two types of glial cells: astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently.

Section Summary

The basic building blocks of complex animals are four primary tissues. These are combined to form organs, which have a specific, specialized function within the body, such as the skin or kidney. Organs are organized together to perform common functions in the form of systems. The four primary tissues are epithelia, connective tissues, muscle tissues, and nervous tissues.

Art Connections

Exercise:

Problem:

Which of the following statements about types of epithelial cells is false?

    a. Simple columnar epithelial cells line the tissue of the lung.
    b. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
    c. Pseudostratisfied columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
    d. Transitional epithelia change in thickness depending on how full the bladder is.

Solution:

A

Review Questions

Exercise:

Problem: Which type of epithelial cell is best adapted to aid diffusion?

    a. squamous
    b. cuboidal
    c. columnar
    d. transitional

Solution:

A

Exercise:

Problem: Which type of epithelial cell is found in glands?

a. squamous
b. cuboidal
c. columnar
d. transitional

Solution:

B

Exercise:

Problem: Which type of epithelial cell is found in the urinary bladder?

a. squamous
b. cuboidal
c. columnar
d. transitional

Solution:

D

Exercise:

Problem: Which type of connective tissue has the most fibers?

a. loose connective tissue
b. fibrous connective tissue
c. cartilage
d. bone

Solution:

B

Exercise:

Problem:

Which type of connective tissue has a mineralized different matrix?

  a. loose connective tissue
  b. fibrous connective tissue
  c. cartilage
  d. bone

Solution:

D

Exercise:

Problem:

The cell found in bone that breaks it down is called an _____.

  a. osteoblast
  b. osteocyte
  c. osteoclast
  d. osteon

Solution:

C

Exercise:

Problem:

The cell found in bone that makes the bone is called an _____.

a. osteoblast
b. osteocyte
c. osteoclast
d. osteon

Solution:

A

Exercise:

Problem: Plasma is the _____.

a. fibers in blood
b. matrix of blood
c. cell that phagocytizes bacteria
d. cell fragment found in the tissue

Solution:

B

Exercise:

Problem:

The type of muscle cell under voluntary control is the _____.

a. smooth muscle
b. skeletal muscle
c. cardiac muscle
d. visceral muscle

Solution:

B

Exercise:

Problem: The part of a neuron that contains the nucleus is the

 a. cell body
 b. dendrite
 c. axon
 d. glial

Solution:

A

Free Response

Exercise:

Problem:

How can squamous epithelia both facilitate diffusion and prevent damage from abrasion?

Solution:

Squamous epithelia can be either simple or stratified. As a single layer of cells, it presents a very thin epithelia that minimally inhibits diffusion. As a stratified epithelia, the surface cells can be sloughed off and the cells in deeper layers protect the underlying tissues from damage.

Exercise:

Problem: What are the similarities between cartilage and bone?

Solution:

Both contain cells other than the traditional fibroblast. Both have cells that lodge in spaces within the tissue called lacunae. Both collagen and elastic fibers are found in bone and cartilage. Both tissues participate in vertebrate skeletal development and formation.

Glossary

canaliculus
> microchannel that connects the lacunae and aids diffusion between cells

cartilage
> type of connective tissue with a large amount of ground substance matrix, cells called chondrocytes, and some amount of fibers

chondrocyte
> cell found in cartilage

columnar epithelia
> epithelia made of cells taller than they are wide, specialized in absorption

connective tissue
> type of tissue made of cells, ground substance matrix, and fibers

cuboidal epithelia
> epithelia made of cube-shaped cells, specialized in glandular functions

epithelial tissue
> tissue that either lines or covers organs or other tissues

fibrous connective tissue
> type of connective tissue with a high concentration of fibers

lacuna
> space in cartilage and bone that contains living cells

loose (areolar) connective tissue
: type of connective tissue with small amounts of cells, matrix, and fibers; found around blood vessels

matrix
: component of connective tissue made of both living and non-living (ground substances) cells

osteon
: subunit of compact bone

pseudostratified
: layer of epithelia that appears multilayered, but is a simple covering

simple epithelia
: single layer of epithelial cells

squamous epithelia
: type of epithelia made of flat cells, specialized in aiding diffusion or preventing abrasion

stratified epithelia
: multiple layers of epithelial cells

trabecula
: tiny plate that makes up spongy bone and gives it strength

transitional epithelia
: epithelia that can transition for appearing multilayered to simple; also called uroepithelial

Homeostasis
By the end of this section, you will be able to:

- Define homeostasis
- Describe the factors affecting homeostasis
- Discuss positive and negative feedback mechanisms used in homeostasis
- Describe thermoregulation of endothermic and ectothermic animals

Animal organs and organ systems constantly adjust to internal and external changes through a process called homeostasis ("steady state"). These changes might be in the level of glucose or calcium in blood or in external temperatures. **Homeostasis** means to maintain dynamic equilibrium in the body. It is dynamic because it is constantly adjusting to the changes that the body's systems encounter. It is equilibrium because body functions are kept within specific ranges. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium.

Homeostatic Process

The goal of homeostasis is the maintenance of equilibrium around a point or value called a **set point**. While there are normal fluctuations from the set point, the body's systems will usually attempt to go back to this point. A change in the internal or external environment is called a stimulus and is detected by a receptor; the response of the system is to adjust the deviation parameter toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If the blood's glucose rises after a meal, adjustments are made to lower the blood glucose level by getting the nutrient into tissues that need it or to store it for later use.

Control of Homeostasis

When a change occurs in an animal's environment, an adjustment must be made. The receptor senses the change in the environment, then sends a signal to the control center (in most cases, the brain) which in turn generates a response that is signaled to an effector. The effector is a muscle (that contracts or relaxes) or a gland that secretes. Homeostatsis is

maintained by negative feedback loops. Positive feedback loops actually push the organism further out of homeostasis, but may be necessary for life to occur. Homeostasis is controlled by the nervous and endocrine system of mammals.

Negative Feedback Mechanisms

Any homeostatic process that changes the direction of the stimulus is a **negative feedback loop**. It may either increase or decrease the stimulus, but the stimulus is not allowed to continue as it did before the receptor sensed it. In other words, if a level is too high, the body does something to bring it down, and conversely, if a level is too low, the body does something to make it go up. Hence the term negative feedback. An example is animal maintenance of blood glucose levels. When an animal has eaten, blood glucose levels rise. This is sensed by the nervous system. Specialized cells in the pancreas sense this, and the hormone insulin is released by the endocrine system. Insulin causes blood glucose levels to decrease, as would be expected in a negative feedback system, as illustrated in [link]. However, if an animal has not eaten and blood glucose levels decrease, this is sensed in another group of cells in the pancreas, and the hormone glucagon is released causing glucose levels to increase. This is still a negative feedback loop, but not in the direction expected by the use of the term "negative." Another example of an increase as a result of the feedback loop is the control of blood calcium. If calcium levels decrease, specialized cells in the parathyroid gland sense this and release parathyroid hormone (PTH), causing an increased absorption of calcium through the intestines and kidneys and, possibly, the breakdown of bone in order to liberate calcium. The effects of PTH are to raise blood levels of the element. Negative feedback loops are the predominant mechanism used in homeostasis.
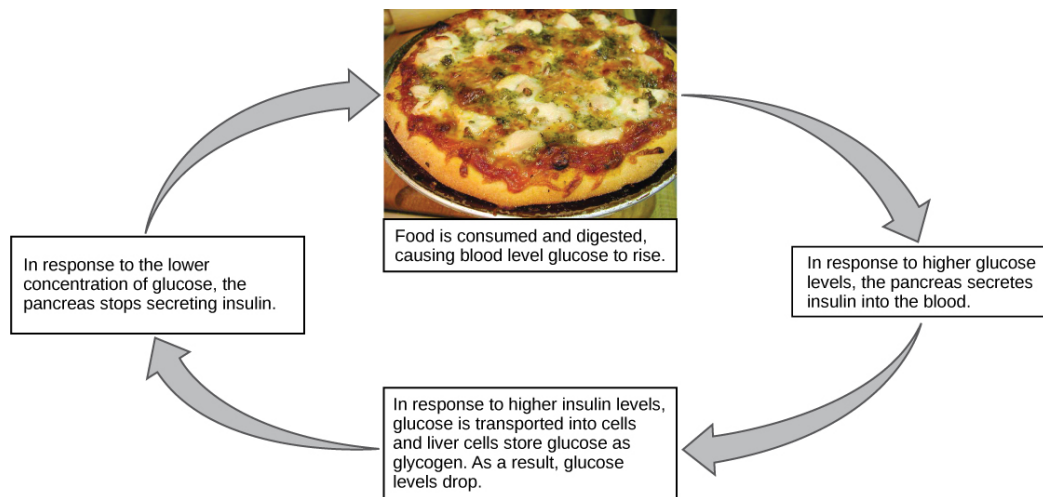
Blood sugar levels are controlled by a negative feedback loop. (credit: modification of work by Jon Sullivan)

Positive Feedback Loop

A **positive feedback loop** maintains the direction of the stimulus, possibly accelerating it. Few examples of positive feedback loops exist in animal bodies, but one is found in the cascade of chemical reactions that result in blood clotting, or coagulation. As one clotting factor is activated, it activates the next factor in sequence until a fibrin clot is achieved. The direction is maintained, not changed, so this is positive feedback. Another example of positive feedback is uterine contractions during childbirth, as illustrated in [link]. The hormone oxytocin, made by the endocrine system, stimulates the contraction of the uterus. This produces pain sensed by the nervous system. Instead of lowering the oxytocin and causing the pain to subside, more oxytocin is produced until the contractions are powerful enough to produce childbirth.

Note:
Art Connection

The baby pushes against the cervix, causing it to stretch.

Uterus

Oxytocin causes the uterus to contract.

Stretching of the cervix causes nerve impulses to be sent to the brain.

Umbilical cord

Cervix

The brain stimulates the pituitary to release oxytocin.
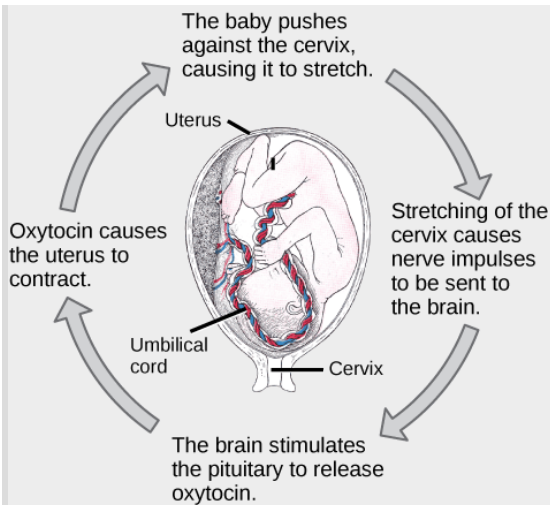
The birth of a human infant is the result of positive feedback.

State whether each of the following processes is regulated by a positive feedback loop or a negative feedback loop.

a. A person feels satiated after eating a large meal.
b. The blood has plenty of red blood cells. As a result, erythropoietin, a hormone that stimulates the production of new red blood cells, is no longer released from the kidney.

Set Point

It is possible to adjust a system's set point. When this happens, the feedback loop works to maintain the new setting. An example of this is blood pressure: over time, the normal or set point for blood pressure can increase as a result of continued increases in blood pressure. The body no longer recognizes the elevation as abnormal and no attempt is made to return to the lower set point. The result is the maintenance of an elevated blood pressure that can have harmful effects on the body. Medication can lower blood

pressure and lower the set point in the system to a more healthy level. This is called a process of **alteration** of the set point in a feedback loop.

Changes can be made in a group of body organ systems in order to maintain a set point in another system. This is called **acclimatization**. This occurs, for instance, when an animal migrates to a higher altitude than it is accustomed to. In order to adjust to the lower oxygen levels at the new altitude, the body increases the number of red blood cells circulating in the blood to ensure adequate oxygen delivery to the tissues. Another example of acclimatization is animals that have seasonal changes in their coats: a heavier coat in the winter ensures adequate heat retention, and a light coat in summer assists in keeping body temperature from rising to harmful levels.

Note:
Link to Learning

Feedback mechanisms can be understood in terms of driving a race car along a track: watch a short video lesson on positive and negative feedback loops.
https://www.openstaxcollege.org/l/feedback_loops

Homeostasis: Thermoregulation

Body temperature affects body activities. Generally, as body temperature rises, enzyme activity rises as well. For every ten degree centigrade rise in temperature, enzyme activity doubles, up to a point. Body proteins, including enzymes, begin to denature and lose their function with high heat

(around 50°C for mammals). Enzyme activity will decrease by half for every ten degree centigrade drop in temperature, to the point of freezing, with a few exceptions. Some fish can withstand freezing solid and return to normal with thawing.

Endotherms and Ectotherms

Animals can be divided into two groups: some maintain a constant body temperature in the face of differing environmental temperatures, while others have a body temperature that is the same as their environment and thus varies with the environment. Animals that do not control their body temperature are ectotherms. This group has been called cold-blooded, but the term may not apply to an animal in the desert with a very warm body temperature. In contrast to ectotherms, which rely on external temperatures to set their body temperatures, poikilotherms are animals with constantly varying internal temperatures. An animal that maintains a constant body temperature in the face of environmental changes is called a homeotherm. Endotherms are animals that rely on internal sources for body temperature but which can exhibit extremes in temperature. These animals are able to maintain a level of activity at cooler temperature, which an ectotherm cannot due to differing enzyme levels of activity.

Heat can be exchanged between an animal and its environment through four mechanisms: radiation, evaporation, convection, and conduction ([link]). Radiation is the emission of electromagnetic "heat" waves. Heat comes from the sun in this manner and radiates from dry skin the same way. Heat can be removed with liquid from a surface during evaporation. This occurs when a mammal sweats. Convection currents of air remove heat from the surface of dry skin as the air passes over it. Heat will be conducted from one surface to another during direct contact with the surfaces, such as an animal resting on a warm rock.

(a) Radiation

(b) Evaporation

(c) Convection

(d) Conduction

Heat can be exchanged by four mechanisms: (a) radiation, (b) evaporation, (c) convection, or (d) conduction. (credit b: modification of work by "Kullez"/Flickr; credit c: modification of work by Chad Rosenthal; credit d: modification of work by "stacey.d"/Flickr)

Heat Conservation and Dissipation

Animals conserve or dissipate heat in a variety of ways. In certain climates, endothermic animals have some form of insulation, such as fur, fat, feathers, or some combination thereof. Animals with thick fur or feathers create an insulating layer of air between their skin and internal organs. Polar bears and seals live and swim in a subfreezing environment and yet maintain a constant, warm, body temperature. The arctic fox, for example, uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals have a residual effect from shivering and increased muscle activity: arrector pili muscles cause "goose bumps," causing small hairs to stand up when the individual is cold; this has the intended effect of increasing body temperature. Mammals use layers of fat to achieve the same end. Loss of significant amounts of body fat will compromise an individual's ability to conserve heat.

Endotherms use their circulatory systems to help maintain body temperature. Vasodilation brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, which helps to cool the body. Vasoconstriction reduces blood flow in peripheral blood vessels, forcing blood toward the core and the vital organs found there, and conserving heat. Some animals have adaptions to their circulatory system that enable them to transfer heat from arteries to veins, warming blood returning to the heart. This is called a countercurrent heat exchange; it prevents the cold venous blood from cooling the heart and other internal organs. This adaption can be shut down in some animals to prevent overheating the internal organs. The countercurrent adaption is found in many animals, including dolphins, sharks, bony fish, bees, and hummingbirds. In contrast, similar adaptations can help cool endotherms when needed, such as dolphin flukes and elephant ears.

Some ectothermic animals use changes in their behavior to help regulate body temperature. For example, a desert ectothermic animal may simply seek cooler areas during the hottest part of the day in the desert to keep from getting too warm. The same animals may climb onto rocks to capture heat during a cold desert night. Some animals seek water to aid evaporation

in cooling them, as seen with reptiles. Other ectotherms use group activity such as the activity of bees to warm a hive to survive winter.

Many animals, especially mammals, use metabolic waste heat as a heat source. When muscles are contracted, most of the energy from the ATP used in muscle actions is wasted energy that translates into heat. Severe cold elicits a shivering reflex that generates heat for the body. Many species also have a type of adipose tissue called brown fat that specializes in generating heat.

Neural Control of Thermoregulation

The nervous system is important to **thermoregulation**, as illustrated in [link]. The processes of homeostasis and temperature control are centered in the hypothalamus of the advanced animal brain.

Note:
Art Connection
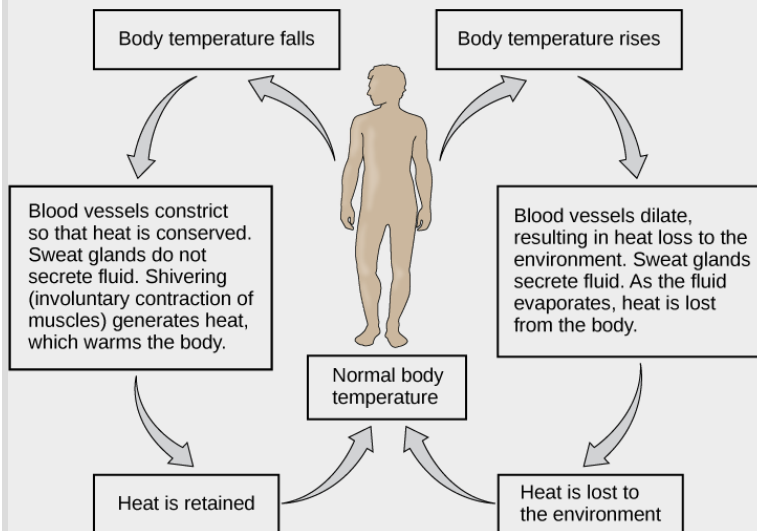
The body is able to regulate temperature in response to signals from the nervous system.

When bacteria are destroyed by leuckocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

The hypothalamus maintains the set point for body temperature through reflexes that cause vasodilation and sweating when the body is too warm, or vasoconstriction and shivering when the body is too cold. It responds to chemicals from the body. When a bacterium is destroyed by phagocytic leukocytes, chemicals called endogenous pyrogens are released into the blood. These pyrogens circulate to the hypothalamus and reset the thermostat. This allows the body's temperature to increase in what is commonly called a fever. An increase in body temperature causes iron to be conserved, which reduces a nutrient needed by bacteria. An increase in body heat also increases the activity of the animal's enzymes and protective cells while inhibiting the enzymes and activity of the invading microorganisms. Finally, heat itself may also kill the pathogen. A fever that was once thought to be a complication of an infection is now understood to be a normal defense mechanism.

Section Summary

Homeostasis is a dynamic equilibrium that is maintained in body tissues and organs. It is dynamic because it is constantly adjusting to the changes that the systems encounter. It is in equilibrium because body functions are kept within a normal range, with some fluctuations around a set point for the processes.

Art Connections

Exercise:

  Problem:

  [link] State whether each of the following processes are regulated by a positive feedback loop or a negative feedback loop.

a. A person feels satiated after eating a large meal.
b. The blood has plenty of red blood cells. As a result, erythropoietin, a hormone that stimulates the production of new red blood cells, is no longer released from the kidney.

Solution:

[link] Both processes are the result of negative feedback loops. Negative feedback loops, which tend to keep a system at equilibrium, are more common than positive feedback loops.

Exercise:

Problem:

[link] When bacteria are destroyed by leuckocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

Solution:

[link] Pyrogens increase body temperature by causing the blood vessels to constrict, inducing shivering, and stopping sweat glands from secreting fluid.

Review Questions

Exercise:

Problem:

When faced with a sudden drop in environmental temperature, an endothermic animal will:

a. experience a drop in its body temperature
b. wait to see if it goes lower
c. increase muscle activity to generate heat

d. add fur or fat to increase insulation

Solution:

C

Exercise:

Problem: Which is an example of negative feedback?

a. lowering of blood glucose after a meal
b. blood clotting after an injury
c. lactation during nursing
d. uterine contractions during labor

Solution:

A

Exercise:

Problem:

Which method of heat exchange occurs during direct contact between the source and animal?

a. radiation
b. evaporation
c. convection
d. conduction

Solution:

D

Exercise:

Problem: The body's thermostat is located in the _____.

    a. homeostatic receptor
    b. hypothalamus
    c. medulla
    d. vasodilation center

Solution:

B

Free Response

Exercise:

Problem:

Why are negative feedback loops used to control body homeostasis?

Solution:

An adjustment to a change in the internal or external environment requires a change in the direction of the stimulus. A negative feedback loop accomplishes this, while a positive feedback loop would continue the stimulus and result in harm to the animal.

Exercise:

Problem: Why is a fever a "good thing" during a bacterial infection?

Solution:

Mammalian enzymes increase activity to the point of denaturation, increasing the chemical activity of the cells involved. Bacterial enzymes have a specific temperature for their most efficient activity and are inhibited at either higher or lower temperatures. Fever results

in an increase in the destruction of the invading bacteria by increasing the effectiveness of body defenses and an inhibiting bacterial metabolism.

Exercise:

Problem:

How is a condition such as diabetes a good example of the failure of a set point in humans?

Solution:

Diabetes is often associated with a lack in production of insulin. Without insulin, blood glucose levels go up after a meal, but never go back down to normal levels.

Glossary

acclimatization
    alteration in a body system in response to environmental change

alteration
    change of the set point in a homeostatic system

homeostasis
    dynamic equilibrium maintaining appropriate body functions

negative feedback loop
    feedback to a control mechanism that increases or decreases a stimulus instead of maintaining it

positive feedback loop
    feedback to a control mechanism that continues the direction of a stimulus

set point
    midpoint or target point in homeostasis

thermoregulation
    regulation of body temperature

Introduction
class="introduction"

For humans, fruits and vegetables are important in maintaining a balanced diet. (credit: modification of work by Julie Rybarczyk)

All living organisms need nutrients to survive. While plants can obtain the molecules required for cellular function through the process of photosynthesis, most animals obtain their nutrients by the consumption of other organisms. At the cellular level, the biological molecules necessary for animal function are amino acids, lipid molecules, nucleotides, and simple sugars. However, the food consumed consists of protein, fat, and complex carbohydrates. Animals must convert these macromolecules into the simple molecules required for maintaining cellular functions, such as assembling new molecules, cells, and tissues. The conversion of the food consumed to the nutrients required is a multi-step process involving digestion and absorption. During digestion, food particles are broken down to smaller components, and later, they are absorbed by the body.

One of the challenges in human nutrition is maintaining a balance between food intake, storage, and energy expenditure. Imbalances can have serious health consequences. For example, eating too much food while not expending much energy leads to obesity, which in turn will increase the risk of developing illnesses such as type-2 diabetes and cardiovascular disease. The recent rise in obesity and related diseases makes understanding the role of diet and nutrition in maintaining good health all the more important.

Digestive Systems
By the end of this section, you will be able to:

- Explain the processes of digestion and absorption
- Compare and contrast different types of digestive systems
- Explain the specialized functions of the organs involved in processing food in the body
- Describe the ways in which organs work together to digest food and absorb nutrients

Animals obtain their nutrition from the consumption of other organisms. Depending on their diet, animals can be classified into the following categories: plant eaters (herbivores), meat eaters (carnivores), and those that eat both plants and animals (omnivores). The nutrients and macromolecules present in food are not immediately accessible to the cells. There are a number of processes that modify food within the animal body in order to make the nutrients and organic molecules accessible for cellular function. As animals evolved in complexity of form and function, their digestive systems have also evolved to accommodate their various dietary needs.

Herbivores, Omnivores, and Carnivores

Herbivores are animals whose primary food source is plant-based. Examples of herbivores, as shown in [link] include vertebrates like deer, koalas, and some bird species, as well as invertebrates such as crickets and caterpillars. These animals have evolved digestive systems capable of handling large amounts of plant material. Herbivores can be further classified into frugivores (fruit-eaters), granivores (seed eaters), nectivores (nectar feeders), and folivores (leaf eaters).

Herbivores, like this (a) mule deer and (b) monarch caterpillar, eat primarily plant material. (credit a: modification of work by Bill Ebbesen; credit b: modification of work by Doug Bowman)

Carnivores are animals that eat other animals. The word carnivore is derived from Latin and literally means "meat eater." Wild cats such as lions, shown in [link]**a** and tigers are examples of vertebrate carnivores, as are snakes and sharks, while invertebrate carnivores include sea stars, spiders, and ladybugs, shown in [link]**b**. Obligate carnivores are those that rely entirely on animal flesh to obtain their nutrients; examples of obligate carnivores are members of the cat family, such as lions and cheetahs. Facultative carnivores are those that also eat non-animal food in addition to animal food. Note that there is no clear line that differentiates facultative carnivores from omnivores; dogs would be considered facultative carnivores.

Carnivores like the (a) lion eat primarily meat. The (b) ladybug is also a carnivore that consumes small insects called aphids. (credit a: modification of work by Kevin Pluck; credit b: modification of work by Jon Sullivan)

Omnivores are animals that eat both plant- and animal-derived food. In Latin, omnivore means to eat everything. Humans, bears (shown in [link]**a**), and chickens are example of vertebrate omnivores; invertebrate omnivores include cockroaches and crayfish (shown in [link]**b**).
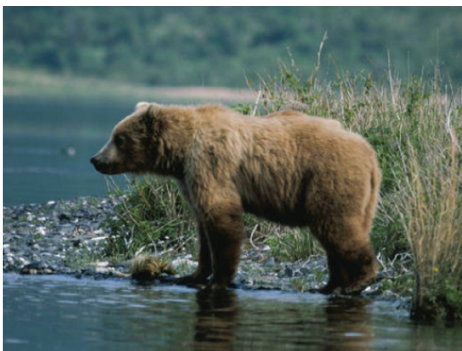
Omnivores like the (a) bear and (b) crayfish eat both plant and animal based food. (credit a: modification of work by Dave Menke; credit b: modification of work by Jon Sullivan)

Invertebrate Digestive Systems

Animals have evolved different types of digestive systems to aid in the digestion of the different foods they consume. The simplest example is that of a **gastrovascular cavity** and is found in organisms with only one opening for digestion. Platyhelminthes (flatworms), Ctenophora (comb jellies), and Cnidaria (coral, jelly fish, and sea anemones) use this type of digestion. Gastrovascular cavities, as shown in [link]**a**, are typically a blind tube or cavity with only one opening, the "mouth", which also serves as an "anus". Ingested material enters the mouth and passes through a hollow, tubular cavity. Cells within the cavity secrete digestive enzymes that break down the food. The food particles are engulfed by the cells lining the gastrovascular cavity.

The **alimentary canal**, shown in [link]**b**, is a more advanced system: it consists of one tube with a mouth at one end and an anus at the other. Earthworms are an example of an animal with an alimentary canal. Once the food is ingested through the mouth, it passes through the esophagus and is stored in an organ called the crop; then it passes into the gizzard where it is churned and digested. From the gizzard, the food passes through the intestine, the nutrients are absorbed, and the waste is eliminated as feces, called castings, through the anus.

Mouth

Gastrovascular
cavity

Mouth

(a) A gastrovascular cavity has one opening.

Mouth   Pharynx   Intestine

Anus

(b) An alimentary canal has two openings.
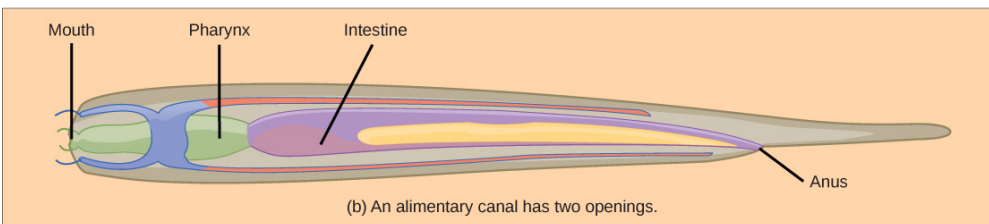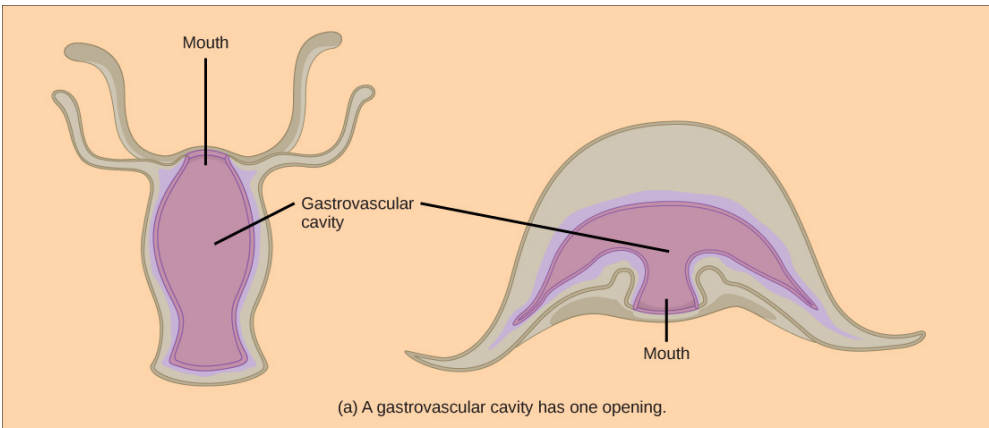
(a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food, and an anus for eliminating waste, as shown in this nematode.

Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating unmasticated food.

Monogastric: Single-chambered Stomach

As the word **monogastric** suggests, this type of digestive system consists of one ("mono") stomach chamber ("gastric"). Humans and many animals have a monogastric digestive system as illustrated in [link]**ab**. The process of digestion begins with the mouth and the intake of food. The teeth play an important role in masticating (chewing) or physically breaking down food into smaller particles. The enzymes present in saliva also begin to chemically break down food. The esophagus is a long tube that connects the mouth to the stomach. Using peristalsis, or wave-like smooth muscle contractions, the muscles of the esophagus push the food towards the stomach. In order to speed up the actions of enzymes in the stomach, the stomach is an extremely acidic environment, with a pH between 1.5 and 2.5. The gastric juices, which include enzymes in the stomach, act on the food particles and continue the process of digestion. Further breakdown of food takes place in the small intestine where enzymes produced by the liver, the small intestine, and the pancreas continue the process of digestion. The nutrients are absorbed into the blood stream across the epithelial cells lining the walls of the small intestines. The waste material travels on to the large intestine where water is absorbed and the drier waste material is compacted into feces; it is stored until it is excreted through the rectum.

(a) Human digestive system   (b) Rabbit digestive system
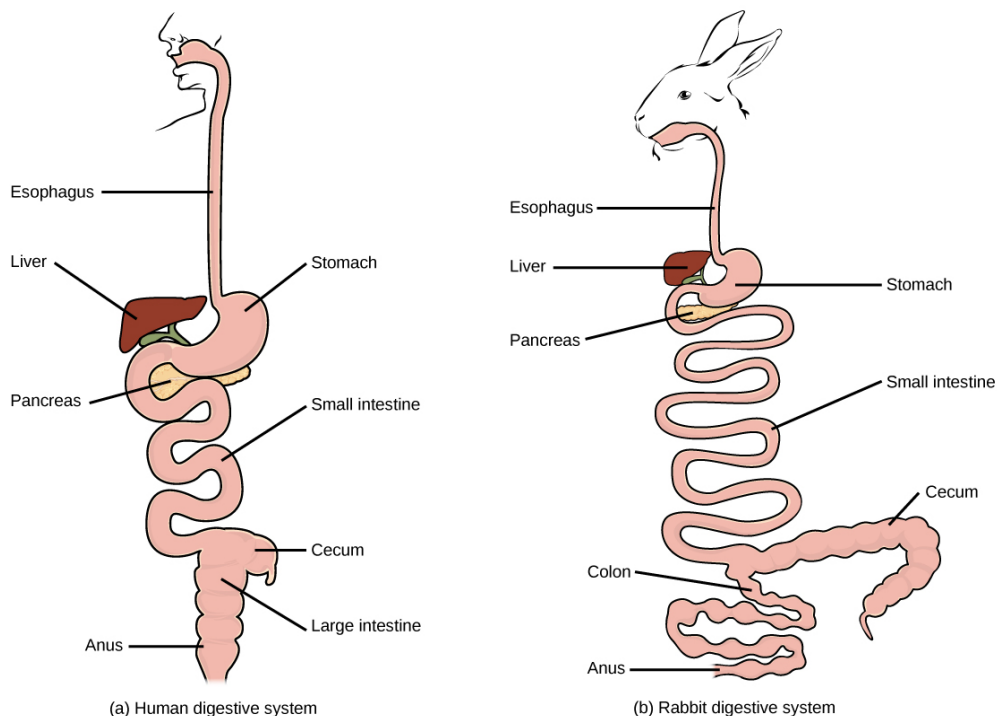
(a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients. Rabbits digest their food twice: the first time food passes through the digestive system, it collects in the cecum, and then it passes as soft feces called cecotrophes. The rabbit re-ingests these cecotrophes to further digest them.

Avian

Birds face special challenges when it comes to obtaining nutrition from food. They do not have teeth and so their digestive system, shown in [link], must be able to process un-masticated food. Birds have evolved a variety of beak types that reflect the vast variety in their diet, ranging from seeds and insects to fruits and nuts. Because most birds fly, their metabolic rates are high in order to efficiently process food and keep their body weight low. The stomach of birds has two chambers: the **proventriculus**, where gastric juices are produced to digest the food before it enters the stomach, and the **gizzard**, where the food is stored, soaked, and mechanically ground. The undigested material forms food pellets that are sometimes regurgitated. Most of the chemical digestion and absorption happens in the intestine and the waste is excreted through the cloaca.
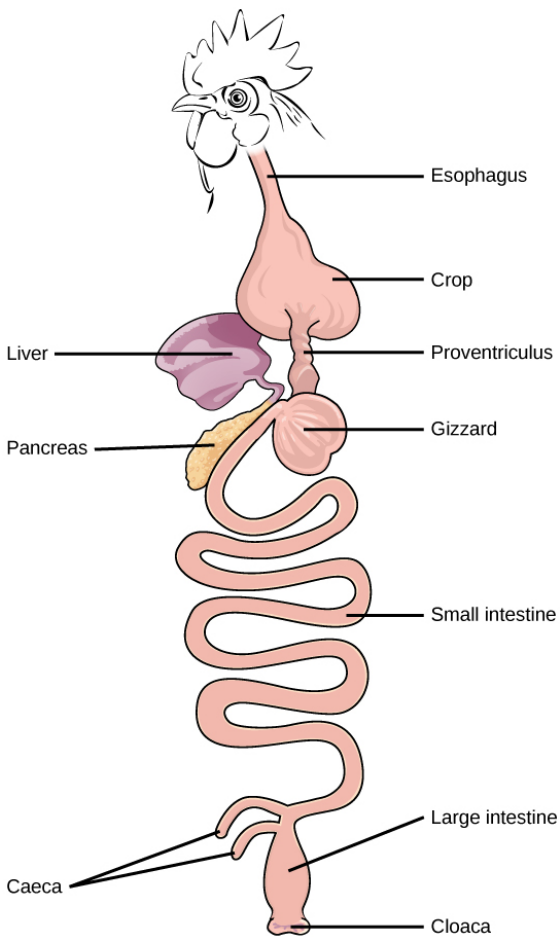
The avian esophagus has a pouch, called a crop, which stores food. Food passes from the crop to the first of two stomachs, called the proventriculus, which contains digestive juices that break down food. From the proventriculus, the food enters the second stomach, called the gizzard, which grinds food. Some birds swallow stones or grit, which are stored in the gizzard, to aid the grinding process. Birds do not have separate

openings to excrete urine and feces. Instead, uric acid from the kidneys is secreted into the large intestine and combined with waste from the digestive process. This waste is excreted through an opening called the cloaca.

Ruminants

Ruminants are mainly herbivores like cows, sheep, and goats, whose entire diet consists of eating large amounts of **roughage** or fiber. They have evolved digestive systems that help them digest vast amounts of cellulose. An interesting feature of the ruminants' mouth is that they do not have

upper incisor teeth. They use their lower teeth, tongue and lips to tear and chew their food. From the mouth, the food travels to the esophagus and on to the stomach.

To help digest the large amount of plant material, the stomach of the ruminants is a multi-chambered organ, as illustrated in [link]. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that break down cellulose and ferment ingested food. The abomasum is the "true" stomach and is the equivalent of the monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary to digest plant material in ruminants. The fermentation process produces large amounts of gas in the stomach chamber, which must be eliminated. As in other animals, the small intestine plays an important role in nutrient absorption, and the large intestine helps in the elimination of waste.
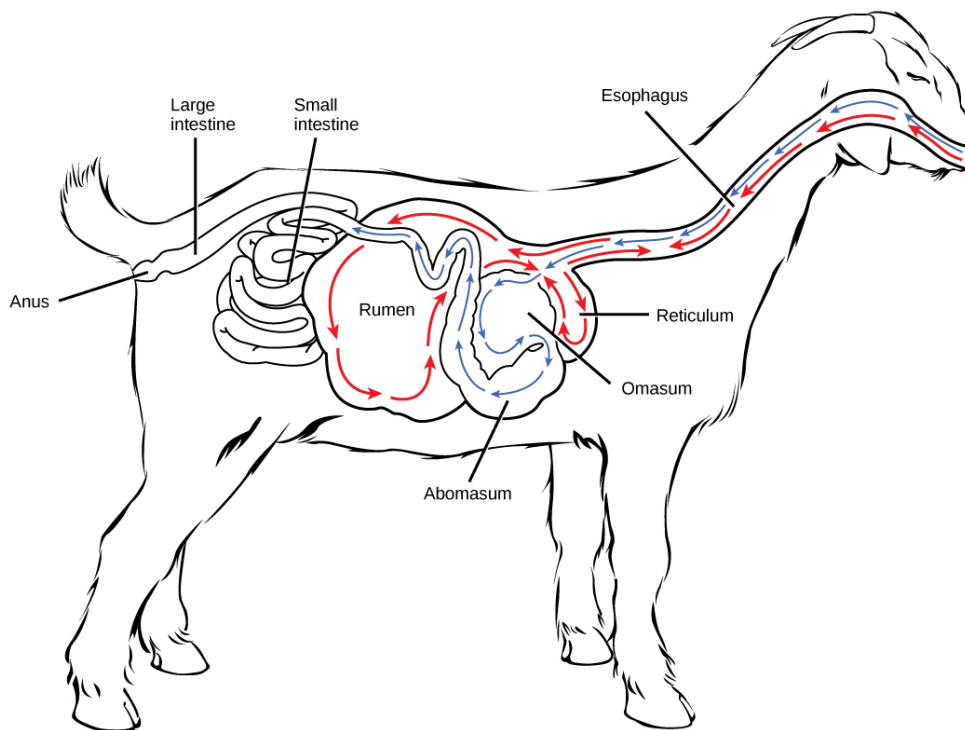
Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the

reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the omasum, which removes water. The cud then passes onto the fourth stomach, the abomasum, where it is digested by enzymes produced by the ruminant.

Pseudo-ruminants

Some animals, such as camels and alpacas, are pseudo-ruminants. They eat a lot of plant material and roughage. Digesting plant material is not easy because plant cell walls contain the polymeric sugar molecule cellulose. The digestive enzymes of these animals cannot break down cellulose, but microorganisms present in the digestive system can. Therefore, the digestive system must be able to handle large amounts of roughage and break down the cellulose. Pseudo-ruminants have a three-chamber stomach in the digestive system. However, their cecum—a pouched organ at the beginning of the large intestine containing many microorganisms that are necessary for the digestion of plant materials—is large and is the site where the roughage is fermented and digested. These animals do not have a rumen but have an omasum, abomasum, and reticulum.

Parts of the Digestive System

The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms.

Oral Cavity

The oral cavity, or mouth, is the point of entry of food into the digestive system, illustrated in [link]. The food consumed is broken into smaller

particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

The extensive chemical process of digestion begins in the mouth. As food is being chewed, saliva, produced by the salivary glands, mixes with the food. Saliva is a watery substance produced in the mouths of many animals. There are three major glands that secrete saliva—the parotid, the submandibular, and the sublingual. Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains immunoglobulins and lysozymes, which have antibacterial action to reduce tooth decay by inhibiting growth of some bacteria. Saliva also contains an enzyme called **salivary amylase** that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme called **lipase** is produced by the cells in the tongue. Lipases are a class of enzymes that can break down triglycerides. The lingual lipase begins the breakdown of fat components in the food. The chewing and wetting action provided by the teeth and saliva prepare the food into a mass called the **bolus** for swallowing. The tongue helps in swallowing—moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the trachea, which leads to the lungs, and the esophagus, which leads to the stomach. The trachea has an opening called the glottis, which is covered by a cartilaginous flap called the epiglottis. When swallowing, the epiglottis closes the glottis and food passes into the esophagus and not the trachea. This arrangement allows food to be kept out of the trachea.
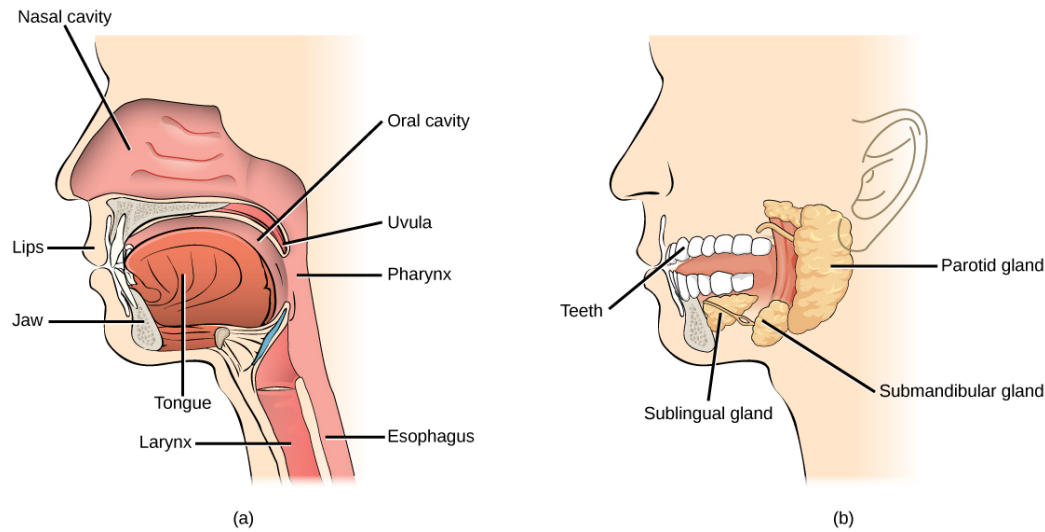
Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by the National Cancer Institute)

Esophagus

The **esophagus** is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave like movements called **peristalsis** that push the food toward the stomach, as illustrated in [link]. The peristalsis wave is unidirectional—it moves food from the mouth to the stomach, and reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.

Direction
of food
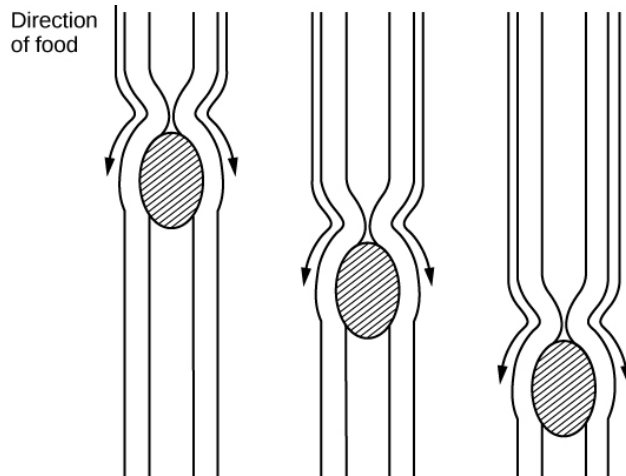
The esophagus transfers food from
the mouth to the stomach through
peristaltic movements.

A ring-like muscle called a **sphincter** forms valves in the digestive system. The gastro-esophageal sphincter is located at the stomach end of the esophagus. In response to swallowing and the pressure exerted by the bolus of food, this sphincter opens, and the bolus enters the stomach. When there is no swallowing action, this sphincter is shut and prevents the contents of the stomach from traveling up the esophagus. Many animals have a true sphincter; however, in humans, there is no true sphincter, but the esophagus remains closed when there is no swallowing action. Acid reflux or "heartburn" occurs when the acidic digestive juices escape into the esophagus.

Stomach

A large part of digestion occurs in the stomach, shown in [link]. The **stomach** is a saclike organ that secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to

up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

Note:
Art Connection
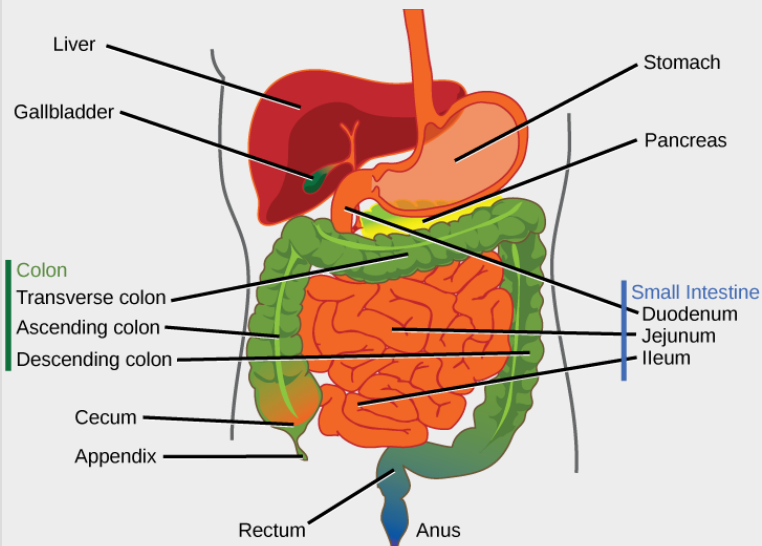
The human stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)

Which of the following statements about the digestive system is false?

a. Chyme is a mixture of food and digestive juices that is produced in the stomach.
b. Food enters the large intestine before the small intestine.
c. In the small intestine, chyme mixes with bile, which emulsifies fats.
d. The stomach is separated from the small intestine by the pyloric sphincter.

The stomach is also the major site for protein digestion in animals other than ruminants. Protein digestion is mediated by an enzyme called pepsin in the stomach chamber. **Pepsin** is secreted by the chief cells in the stomach in an inactive form called **pepsinogen**. Pepsin breaks peptide bonds and cleaves proteins into smaller polypeptides; it also helps activate more pepsinogen, starting a positive feedback mechanism that generates more pepsin. Another cell type—parietal cells—secrete hydrogen and chloride ions, which combine in the lumen to form hydrochloric acid, the primary acidic component of the stomach juices. Hydrochloric acid helps to convert the inactive pepsinogen to pepsin. The highly acidic environment also kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the hydrolysis of protein in the food. Chemical digestion is facilitated by the churning action of the stomach. Contraction and relaxation of smooth muscles mixes the stomach contents about every 20 minutes. The partially digested food and gastric juice mixture is called **chyme**. Chyme passes from the stomach to the small intestine. Further protein digestion takes place in the small intestine. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by the pyloric sphincter.

When digesting protein and some fats, the stomach lining must be protected from getting digested by pepsin. There are two points to consider when describing how the stomach lining is protected. First, as previously mentioned, the enzyme pepsin is synthesized in the inactive form. This protects the chief cells, because pepsinogen does not have the same enzyme functionality of pepsin. Second, the stomach has a thick mucus lining that protects the underlying tissue from the action of the digestive juices. When this mucus lining is ruptured, ulcers can form in the stomach. Ulcers are open wounds in or on an organ caused by bacteria (*Helicobacter pylori*) when the mucus lining is ruptured and fails to reform.

Small Intestine

Chyme moves from the stomach to the small intestine. The **small intestine** is the organ where the digestion of protein, fats, and carbohydrates is

completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the **villi**. The apical surface of each villus has many microscopic projections called microvilli. These structures, illustrated in [link], are lined with epithelial cells on the luminal side and allow for the nutrients to be absorbed from the digested food and absorbed into the blood stream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients. Absorbed nutrients in the blood are carried into the hepatic portal vein, which leads to the liver. There, the liver regulates the distribution of nutrients to the rest of the body and removes toxic substances, including drugs, alcohol, and some pathogens.

Note:
Art Connection

Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nutrients.

Which of the following statements about the small intestine is false?

a. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.

The human small intestine is over 6m long and is divided into three parts: the duodenum, the jejunum, and the ileum. The "C-shaped," fixed part of the small intestine is called the **duodenum** and is shown in [link]. The duodenum is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum. In the duodenum, chyme is mixed with pancreatic juices in an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Pancreatic juices also contain several digestive enzymes. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. **Bile** is produced in the liver and stored and concentrated in the gallbladder. Bile contains bile salts which emulsify lipids while the pancreas produces enzymes that catabolize starches, disaccharides, proteins, and fats. These digestive juices break down the food particles in the chyme into glucose, triglycerides, and amino acids. Some chemical digestion of food takes place in the duodenum. Absorption of fatty acids also takes place in the duodenum.

The second part of the small intestine is called the **jejunum**, shown in [link]. Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. The bulk of chemical digestion and nutrient absorption occurs in the jejunum.

The **ileum**, also illustrated in [link] is the last part of the small intestine and here the bile salts and vitamins are absorbed into blood stream. The undigested food is sent to the colon from the ileum via peristaltic movements of the muscle. The ileum ends and the large intestine begins at the ileocecal valve. The vermiform, "worm-like," appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

The **large intestine**, illustrated in [link], reabsorbs the water from the undigested food material and processes the waste material. The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or "intestinal flora" that aid in the digestive processes. The colon can be divided into four regions, the ascending colon, the transverse colon, the descending colon and the sigmoid colon. The main functions of the colon are to extract the water and mineral salts from undigested food, and to store waste material. Carnivorous mammals have a shorter large intestine compared to herbivorous mammals due to their diet.
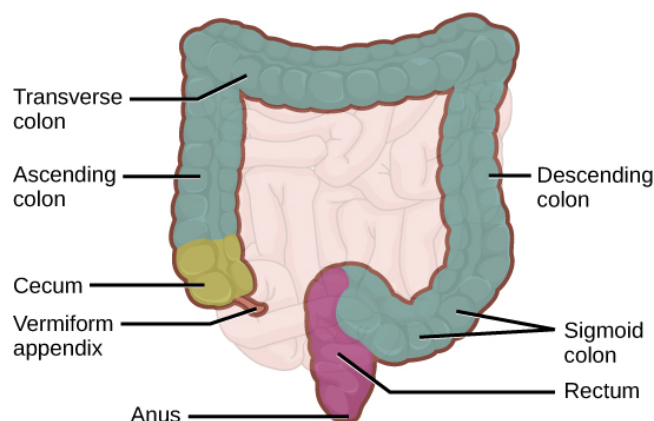
The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

Rectum and Anus

The **rectum** is the terminal end of the large intestine, as shown in [link]. The primary role of the rectum is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The **anus** is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

The organs discussed above are the organs of the digestive tract through which food passes. Accessory organs are organs that add secretions (enzymes) that catabolize food into nutrients. Accessory organs include salivary glands, the liver, the pancreas, and the gallbladder. The liver, pancreas, and gallbladder are regulated by hormones in response to the food consumed.

The **liver** is the largest internal organ in humans and it plays a very important role in digestion of fats and detoxifying blood. The liver produces bile, a digestive juice that is required for the breakdown of fatty components of the food in the duodenum. The liver also processes the vitamins and fats and synthesizes many plasma proteins.

The **pancreas** is another important gland that secretes digestive juices. The chyme produced from the stomach is highly acidic in nature; the pancreatic juices contain high levels of bicarbonate, an alkali that neutralizes the acidic chyme. Additionally, the pancreatic juices contain a large variety of enzymes that are required for the digestion of protein and carbohydrates.

The **gallbladder** is a small organ that aids the liver by storing bile and concentrating bile salts. When chyme containing fatty acids enters the duodenum, the bile is secreted from the gallbladder into the duodenum.

Section Summary

Different animals have evolved different types of digestive systems specialized to meet their dietary needs. Humans and many other animals have monogastric digestive systems with a single-chambered stomach. Birds have evolved a digestive system that includes a gizzard where the food is crushed into smaller pieces. This compensates for their inability to masticate. Ruminants that consume large amounts of plant material have a multi-chambered stomach that digests roughage. Pseudo-ruminants have similar digestive processes as ruminants but do not have the four-compartment stomach. Processing food involves ingestion (eating), digestion (mechanical and enzymatic breakdown of large molecules), absorption (cellular uptake of nutrients), and elimination (removal of undigested waste as feces).

Many organs work together to digest food and absorb nutrients. The mouth is the point of ingestion and the location where both mechanical and chemical breakdown of food begins. Saliva contains an enzyme called amylase that breaks down carbohydrates. The food bolus travels through the esophagus by peristaltic movements to the stomach. The stomach has an extremely acidic environment. An enzyme called pepsin digests protein in the stomach. Further digestion and absorption take place in the small intestine. The large intestine reabsorbs water from the undigested food and stores waste until elimination.

Art Connections

Exercise:

 Problem:

[link] Which of the following statements about the digestive system is false?

   a. Chyme is a mixture of food and digestive juices that is produced in the stomach.
   b. Food enters the large intestine before the small intestine.
   c. In the small intestine, chyme mixes with bile, which emulsifies fats.

d. The stomach is separated from the small intestine by the pyloric sphincter.

Solution:

B

Exercise:

Problem:

Which of the following statements about the small intestine is false?

a. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
b. The inside of the small intestine has many folds, called villi.
c. Microvilli are lined with blood vessels as well as lymphatic vessels.
d. The inside of the small intestine is called the lumen.

Solution:

C

Review Questions

Exercise:

Problem: Which of the following is a pseudo-ruminant?

a. cow
b. pig
c. crow
d. horse

Solution:

D

Exercise:

Problem: Which of the following statements is untrue?

    a. Roughage takes a long time to digest.
    b. Birds eat large quantities at one time so that they can fly long distances.
    c. Cows do not have upper teeth.
    d. In pseudo-ruminants, roughage is digested in the cecum.

Solution:

B

Exercise:

Problem: The acidic nature of chyme is neutralized by _____.

    a. potassium hydroxide
    b. sodium hydroxide
    c. bicarbonates
    d. vinegar

Solution:

C

Exercise:

Problem:

The digestive juices from the liver are delivered to the _____.

a. stomach
b. liver
c. duodenum
d. colon

Solution:

C

Free Response

Exercise:

Problem:

How does the polygastric digestive system aid in digesting roughage?

Solution:

Animals with a polygastric digestive system have a multi-chambered stomach. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that break down the cellulose and ferment the ingested food. The abomasum is the "true" stomach and is the equivalent of a monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary for ruminants to digest plant material.

Exercise:

Problem: How do birds digest their food in the absence of teeth?

Solution:

Birds have a stomach chamber called a gizzard. Here, the food is stored, soaked, and ground into finer particles, often using pebbles.

Once this process is complete, the digestive juices take over in the proventriculus and continue the digestive process.

Exercise:

Problem: What is the role of the accessory organs in digestion?

Solution:

Accessory organs play an important role in producing and delivering digestive juices to the intestine during digestion and absorption. Specifically, the salivary glands, liver, pancreas, and gallbladder play important roles. Malfunction of any of these organs can lead to disease states.

Exercise:

Problem: Explain how the villi and microvilli aid in absorption.

Solution:

The villi and microvilli are folds on the surface of the small intestine. These folds increase the surface area of the intestine and provide more area for the absorption of nutrients.

Glossary

alimentary canal
    tubular digestive system with a mouth and anus

anus
    exit point for waste material

bile
    digestive juice produced by the liver; important for digestion of lipids

bolus

mass of food resulting from chewing action and wetting by saliva

carnivore
animal that consumes animal flesh

chyme
mixture of partially digested food and stomach juices

duodenum
first part of the small intestine where a large part of digestion of carbohydrates and fats occurs

esophagus
tubular organ that connects the mouth to the stomach

gallbladder
organ that stores and concentrates bile

gastrovascular cavity
digestive system consisting of a single opening

gizzard
muscular organ that grinds food

herbivore
animal that consumes strictly plant diet

ileum
last part of the small intestine; connects the small intestine to the large intestine; important for absorption of B-12

jejunum
second part of the small intestine

large intestine
digestive system organ that reabsorbs water from undigested material and processes waste matter

lipase

enzyme that chemically breaks down lipids

liver
    organ that produces bile for digestion and processes vitamins and
    lipids

monogastric
    digestive system that consists of a single-chambered stomach

omnivore
    animal that consumes both plants and animals

pancreas
    gland that secretes digestive juices

pepsin
    enzyme found in the stomach whose main role is protein digestion

pepsinogen
    inactive form of pepsin

peristalsis
    wave-like movements of muscle tissue

proventriculus
    glandular part of a bird's stomach

rectum
    area of the body where feces is stored until elimination

roughage
    component of food that is low in energy and high in fiber

ruminant
    animal with a stomach divided into four compartments

salivary amylase
    enzyme found in saliva, which converts carbohydrates to maltose

small intestine
    organ where digestion of protein, fats, and carbohydrates is completed

sphincter
    band of muscle that controls movement of materials throughout the
    digestive tract

stomach
    saclike organ containing acidic digestive juices

villi
    folds on the inner surface of the small intestine whose role is to
    increase absorption area

Nutrition and Energy Production
By the end of this section, you will be able to:

- Explain why an animal's diet should be balanced and meet the needs of the body
- Define the primary components of food
- Describe the essential nutrients required for cellular function that cannot be synthesized by the animal body
- Explain how energy is produced through diet and digestion
- Describe how excess carbohydrates and energy are stored in the body

Given the diversity of animal life on our planet, it is not surprising that the animal diet would also vary substantially. The animal diet is the source of materials needed for building DNA and other complex molecules needed for growth, maintenance, and reproduction; collectively these processes are called biosynthesis. The diet is also the source of materials for ATP production in the cells. The diet must be balanced to provide the minerals and vitamins that are required for cellular function.

Food Requirements

What are the fundamental requirements of the animal diet? The animal diet should be well balanced and provide nutrients required for bodily function and the minerals and vitamins required for maintaining structure and regulation necessary for good health and reproductive capability. These requirements for a human are illustrated graphically in [link]
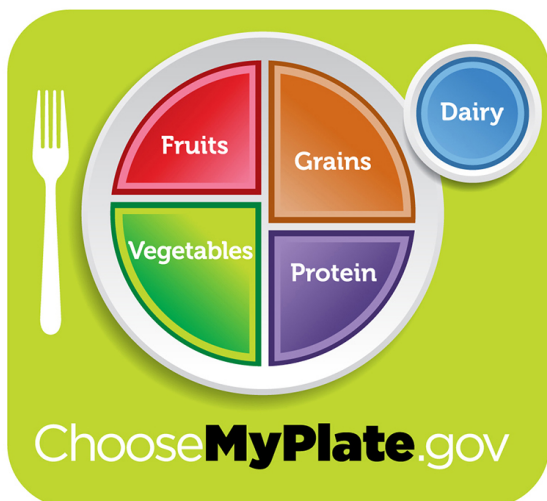
For humans, a balanced diet includes fruits, vegetables, grains, and protein. (credit: USDA)

Organic Precursors

The organic molecules required for building cellular material and tissues must come from food. Carbohydrates or sugars are the primary source of organic carbons in the animal body. During digestion, digestible carbohydrates are ultimately broken down into glucose and used to provide energy through metabolic pathways. Complex carbohydrates, including polysaccharides, can be broken down into glucose through biochemical modification; however, humans do not produce the enzyme cellulase and lack the ability to derive glucose from the polysaccharide cellulose. In humans, these molecules provide the fiber required for moving waste through the large intestine and a healthy colon. The intestinal flora in the human gut are able to extract some nutrition from these plant fibers. The excess sugars in the body are converted into glycogen and stored in the liver and muscles for later use. Glycogen stores are used to fuel prolonged exertions, such as long-distance running, and to provide energy during food shortage. Excess glycogen can be converted to fats, which are stored in the lower layer of the skin of mammals for insulation and energy storage. Excess digestible carbohydrates are stored by mammals in order to survive famine and aid in mobility.

Another important requirement is that of nitrogen. Protein catabolism provides a source of organic nitrogen. Amino acids are the building blocks of proteins and protein breakdown provides amino acids that are used for cellular function. The carbon and nitrogen derived from these become the building block for nucleotides, nucleic acids, proteins, cells, and tissues. Excess nitrogen must be excreted as it is toxic. Fats add flavor to food and promote a sense of satiety or fullness. Fatty foods are also significant sources of energy because one gram of fat contains nine calories. Fats are required in the diet to aid the absorption of fat-soluble vitamins and the production of fat-soluble hormones.

Essential Nutrients

While the animal body can synthesize many of the molecules required for function from the organic precursors, there are some nutrients that need to be consumed from food. These nutrients are termed **essential nutrients**, meaning they must be eaten, and the body cannot produce them.

The omega-3 alpha-linolenic acid and the omega-6 linoleic acid are essential fatty acids needed to make some membrane phospholipids. **Vitamins** are another class of essential organic molecules that are required in small quantities for many enzymes to function and, for this reason, are considered to be co-enzymes. Absence or low levels of vitamins can have a dramatic effect on health, as outlined in [link] and [link]. Both fat-soluble and water-soluble vitamins must be obtained from food. **Minerals**, listed in [link], are inorganic essential nutrients that must be obtained from food. Among their many functions, minerals help in structure and regulation and are considered co-factors. Certain amino acids also must be procured from food and cannot be synthesized by the body. These amino acids are the "essential" amino acids. The human body can synthesize only 11 of the 20 required amino acids; the rest must be obtained from food. The essential amino acids are listed in [link].

Water-soluble Essential Vitamins			
Vitamin	**Function**	**Deficiencies Can Lead To**	**Sources**
Vitamin B_1 (Thiamine)	Needed by the body to process lipids, proteins, and carbohydrates Coenzyme removes CO_2 from organic compounds	Muscle weakness, Beriberi: reduced heart function, CNS problems	Milk, meat, dried beans, whole grains
Vitamin B_2 (Riboflavin)	Takes an active role in metabolism, aiding in the conversion of food to energy (FAD and FMN)	Cracks or sores on the outer surface of the lips (cheliosis); inflammation and redness of the tongue; moist, scaly skin inflammation (seborrheic dermatitis)	Meat, eggs, enriched grains, vegetables

Water-soluble Essential Vitamins			
Vitamin	**Function**	**Deficiencies Can Lead To**	**Sources**
Vitamin B_3 (Niacin)	Used by the body to release energy from carbohydrates and to process alcohol; required for the synthesis of sex hormones; component of coenzyme NAD^+ and $NADP^+$	Pellagra, which can result in dermatitis, diarrhea, dementia, and death	Meat, eggs, grains, nuts, potatoes
Vitamin B_5 (Pantothenic acid)	Assists in producing energy from foods (lipids, in particular); component of coenzyme A	Fatigue, poor coordination, retarded growth, numbness, tingling of hands and feet	Meat, whole grains, milk, fruits, vegetables
Vitamin B_6 (Pyridoxine)	The principal vitamin for processing amino acids and lipids; also helps convert nutrients into energy	Irritability, depression, confusion, mouth sores or ulcers, anemia, muscular twitching	Meat, dairy products, whole grains, orange juice

Water-soluble Essential Vitamins			
Vitamin	**Function**	**Deficiencies Can Lead To**	**Sources**
Vitamin B_7 (Biotin)	Used in energy and amino acid metabolism, fat synthesis, and fat breakdown; helps the body use blood sugar	Hair loss, dermatitis, depression, numbness and tingling in the extremities; neuromuscular disorders	Meat, eggs, legumes and other vegetables
Vitamin B_9 (Folic acid)	Assists the normal development of cells, especially during fetal development; helps metabolize nucleic and amino acids	Deficiency during pregnancy is associated with birth defects, such as neural tube defects and anemia	Leafy green vegetables, whole wheat, fruits, nuts, legumes
Vitamin B_{12} (Cobalamin)	Maintains healthy nervous system and assists with blood cell formation; coenzyme in nucleic acid metabolism	Anemia, neurological disorders, numbness, loss of balance	Meat, eggs, animal products

Water-soluble Essential Vitamins

Vitamin	Function	Deficiencies Can Lead To	Sources
Vitamin C (Ascorbic acid)	Helps maintain connective tissue: bone, cartilage, and dentin; boosts the immune system	Scurvy, which results in bleeding, hair and tooth loss; joint pain and swelling; delayed wound healing	Citrus fruits, broccoli, tomatoes, red sweet bell peppers

Fat-soluble Essential Vitamins

Vitamin	Function	Deficiencies Can Lead To	Sources

Fat-soluble Essential Vitamins			
Vitamin	**Function**	**Deficiencies Can Lead To**	**Sources**
Vitamin A (Retinol)	Critical to the development of bones, teeth, and skin; helps maintain eyesight, enhances the immune system, fetal development, gene expression	Night-blindness, skin disorders, impaired immunity	Dark green leafy vegetables, yellow-orange vegetables fruits, milk, butter
Vitamin D	Critical for calcium absorption for bone development and strength; maintains a stable nervous system; maintains a normal and strong heartbeat; helps in blood clotting	Rickets, osteomalacia, immunity	Cod liver oil, milk, egg yolk

Fat-soluble Essential Vitamins			
Vitamin	**Function**	**Deficiencies Can Lead To**	**Sources**
Vitamin E (Tocopherol)	Lessens oxidative damage of cells,and prevents lung damage from pollutants; vital to the immune system	Deficiency is rare; anemia, nervous system degeneration	Wheat germ oil, unrefined vegetable oils, nuts, seeds, grains
Vitamin K (Phylloquinone)	Essential to blood clotting	Bleeding and easy bruising	Leafy green vegetables, tea

A healthy diet should include a variety of

foods to ensure that needs for essential nutrients are met. (credit: Keith Weller, USDA ARS)

Minerals and Their Function in the Human Body

Mineral	Function	Deficiencies Can Lead To	Sources
*Calcium	Needed for muscle and neuron function; heart health; builds bone and supports synthesis and function of blood cells; nerve function	Osteoporosis, rickets, muscle spasms, impaired growth	Milk, yogurt, fish, green leafy vegetables, legumes
*Chlorine	Needed for production of hydrochloric acid (HCl) in the stomach and nerve function; osmotic balance	Muscle cramps, mood disturbances, reduced appetite	Table salt

Minerals and Their Function in the Human Body			
Mineral	**Function**	**Deficiencies Can Lead To**	**Sources**
Copper (trace amounts)	Required component of many redox enzymes, including cytochrome c oxidase; cofactor for hemoglobin synthesis	Copper deficiency is rare	Liver, oysters, cocoa, chocolate, sesame, nuts
Iodine	Required for the synthesis of thyroid hormones	Goiter	Seafood, iodized salt, dairy products
Iron	Required for many proteins and enzymes, notably hemoglobin, to prevent anemia	Anemia, which causes poor concentration, fatigue, and poor immune function	Red meat, leafy green vegetables, fish (tuna, salmon), eggs, dried fruits, beans, whole grains

Minerals and Their Function in the Human Body			
Mineral	**Function**	**Deficiencies Can Lead To**	**Sources**
*Magnesium	Required co-factor for ATP formation; bone formation; normal membrane functions; muscle function	Mood disturbances, muscle spasms	Whole grains, leafy green vegetables
Manganese (trace amounts)	A cofactor in enzyme functions; trace amounts are required	Manganese deficiency is rare	Common in most foods
Molybdenum (trace amounts)	Acts as a cofactor for three essential enzymes in humans: sulfite oxidase, xanthine oxidase, and aldehyde oxidase	Molybdenum deficiency is rare	
*Phosphorus	A component of bones and teeth; helps regulate acid-base balance; nucleotide synthesis	Weakness, bone abnormalities, calcium loss	Milk, hard cheese, whole grains, meats

Minerals and Their Function in the Human Body			
Mineral	**Function**	**Deficiencies Can Lead To**	**Sources**
*Potassium	Vital for muscles, heart, and nerve function	Cardiac rhythm disturbance, muscle weakness	Legumes, potato skin, tomatoes, bananas
Selenium (trace amounts)	A cofactor essential to activity of antioxidant enzymes like glutathione peroxidase; trace amounts are required	Selenium deficiency is rare	Common in most foods
*Sodium	Systemic electrolyte required for many functions; acid-base balance; water balance; nerve function	Muscle cramps, fatigue, reduced appetite	Table salt
Zinc (trace amounts)	Required for several enzymes such as carboxypeptidase, liver alcohol dehydrogenase, and carbonic anhydrase	Anemia, poor wound healing, can lead to short stature	Common in most foods

Minerals and Their Function in the Human Body			
Mineral	**Function**	**Deficiencies Can Lead To**	**Sources**
*Greater than 200mg/day required			

Essential Amino Acids	
Amino acids that must be consumed	**Amino acids anabolized by the body**
isoleucine	alanine
leucine	selenocysteine
lysine	aspartate
methionine	cysteine
phenylalanine	glutamate
tryptophan	glycine
valine	proline
histidine*	serine
threonine	tyrosine
arginine*	asparagine

Essential Amino Acids	
Amino acids that must be consumed	Amino acids anabolized by the body
*The human body can synthesize histidine and arginine, but not in the quantities required, especially for growing children.	

Food Energy and ATP

Animals need food to obtain energy and maintain homeostasis. Homeostasis is the ability of a system to maintain a stable internal environment even in the face of external changes to the environment. For example, the normal body temperature of humans is 37°C (98.6°F). Humans maintain this temperature even when the external temperature is hot or cold. It takes energy to maintain this body temperature, and animals obtain this energy from food.

The primary source of energy for animals is carbohydrates, mainly glucose. Glucose is called the body's fuel. The digestible carbohydrates in an animal's diet are converted to glucose molecules through a series of catabolic chemical reactions.

Adenosine triphosphate, or ATP, is the primary energy currency in cells; ATP stores energy in phosphate ester bonds. ATP releases energy when the phosphodiester bonds are broken and ATP is converted to ADP and a phosphate group. ATP is produced by the oxidative reactions in the cytoplasm and mitochondrion of the cell, where carbohydrates, proteins, and fats undergo a series of metabolic reactions collectively called cellular respiration. For example, glycolysis is a series of reactions in which glucose is converted to pyruvic acid and some of its chemical potential energy is transferred to NADH and ATP.

ATP is required for all cellular functions. It is used to build the organic molecules that are required for cells and tissues; it provides energy for muscle contraction and for the transmission of electrical signals in the nervous system. When the amount of ATP is available in excess of the body's requirements, the liver uses the excess ATP and excess glucose to produce

molecules called glycogen. Glycogen is a polymeric form of glucose and is stored in the liver and skeletal muscle cells. When blood sugar drops, the liver releases glucose from stores of glycogen. Skeletal muscle converts glycogen to glucose during intense exercise. The process of converting glucose and excess ATP to glycogen and the storage of excess energy is an evolutionarily important step in helping animals deal with mobility, food shortages, and famine.

Note:
Everyday Connection
Obesity
Obesity is a major health concern in the United States, and there is a growing focus on reducing obesity and the diseases it may lead to, such as type-2 diabetes, cancers of the colon and breast, and cardiovascular disease. How does the food consumed contribute to obesity?

Fatty foods are calorie-dense, meaning that they have more calories per unit mass than carbohydrates or proteins. One gram of carbohydrates has four calories, one gram of protein has four calories, and one gram of fat has nine calories. Animals tend to seek lipid-rich food for their higher energy content. The signals of hunger ("time to eat") and satiety ("time to stop eating") are controlled in the hypothalamus region of the brain. Foods that are rich in fatty acids tend to promote satiety more than foods that are rich only in carbohydrates.

Excess carbohydrate and ATP are used by the liver to synthesize glycogen. The pyruvate produced during glycolysis is used to synthesize fatty acids. When there is more glucose in the body than required, the resulting excess pyruvate is converted into molecules that eventually result in the synthesis of fatty acids within the body. These fatty acids are stored in adipose cells—the fat cells in the mammalian body whose primary role is to store fat for later use.

It is important to note that some animals benefit from obesity. Polar bears and seals need body fat for insulation and to keep them from losing body heat during Arctic winters. When food is scarce, stored body fat provides energy for maintaining homeostasis. Fats prevent famine in mammals, allowing them to access energy when food is not available on a daily basis; fats are stored when a large kill is made or lots of food is available.

Section Summary

Animal diet should be balanced and meet the needs of the body. Carbohydrates, proteins, and fats are the primary components of food. Some essential nutrients are required for cellular function but cannot be produced by the animal body. These include vitamins, minerals, some fatty acids, and some amino acids. Food intake in more than necessary amounts is stored as glycogen in the liver and muscle cells, and in fat cells. Excess adipose storage can lead to obesity and serious health problems. ATP is the energy currency of the cell and is obtained from the metabolic pathways. Excess carbohydrates and energy are stored as glycogen in the body.

Review Questions

Exercise:

Problem: Which of the following statements is not true?

    a. Essential nutrients can be synthesized by the body.
    b. Vitamins are required in small quantities for bodily function.
    c. Some amino acids can be synthesized by the body, while others need to be obtained from diet.
    d. Vitamins come in two categories: fat-soluble and water-soluble.

Solution:

A

Exercise:

Problem: Which of the following is a water-soluble vitamin?

    a. vitamin A
    b. vitamin E
    c. vitamin K
    d. vitamin C

Solution:

D

Exercise:

Problem: What is the primary fuel for the body?

    a. carbohydrates
    b. lipids
    c. protein
    d. glycogen

Solution:

A

Exercise:

Problem: Excess glucose is stored as _____.

    a. fat
    b. glucagon
    c. glycogen
    d. it is not stored in the body

Solution:

C

Free Response

Exercise:

Problem: What are essential nutrients?

Solution:

Essential nutrients are those nutrients that must be obtained from the diet because they cannot be produced by the body. Vitamins and minerals are examples of essential nutrients.

Exercise:

Problem: What is the role of minerals in maintaining good health?

Solution:

Minerals—such as potassium, sodium, and calcium—are required for the functioning of many cellular processes, including muscle contraction and nerve conduction. While minerals are required in trace amounts, not having minerals in the diet can be potentially harmful.

Exercise:

Problem: Discuss why obesity is a growing epidemic.

Solution:

In the United States, obesity, particularly childhood obesity, is a growing concern. Some of the contributors to this situation include sedentary lifestyles and consuming more processed foods and less fruits and vegetables. As a result, even young children who are obese can face health concerns.

Exercise:

Problem:

There are several nations where malnourishment is a common occurrence. What may be some of the health challenges posed by malnutrition?

Solution:

Malnutrition, often in the form of not getting enough calories or not enough of the essential nutrients, can have severe consequences. Many malnourished children have vision and dental problems, and over the years may develop many serious health problems.

Glossary

essential nutrient
   nutrient that cannot be synthesized by the body; it must be obtained from food

mineral
   inorganic, elemental molecule that carries out important roles in the body

vitamin
   organic substance necessary in small amounts to sustain life

Digestive System Processes
By the end of this section, you will be able to:

- Describe the process of digestion
- Detail the steps involved in digestion and absorption
- Define elimination
- Explain the role of both the small and large intestines in absorption

Obtaining nutrition and energy from food is a multi-step process. For true animals, the first step is ingestion, the act of taking in food. This is followed by digestion, absorption, and elimination. In the following sections, each of these steps will be discussed in detail.

Ingestion

The large molecules found in intact food cannot pass through the cell membranes. Food needs to be broken into smaller particles so that animals can harness the nutrients and organic molecules. The first step in this process is **ingestion**. Ingestion is the process of taking in food through the mouth. In vertebrates, the teeth, saliva, and tongue play important roles in mastication (preparing the food into bolus). While the food is being mechanically broken down, the enzymes in saliva begin to chemically process the food as well. The combined action of these processes modifies the food from large particles to a soft mass that can be swallowed and can travel the length of the esophagus.

Digestion and Absorption

Digestion is the mechanical and chemical break down of food into small organic fragments. It is important to break down macromolecules into smaller fragments that are of suitable size for absorption across the digestive epithelium. Large, complex molecules of proteins, polysaccharides, and lipids must be reduced to simpler particles such as simple sugar before they can be absorbed by the digestive epithelial cells. Different organs play specific roles in the digestive process. The animal diet needs carbohydrates, protein, and fat, as well as vitamins and inorganic components for nutritional balance. How each of these components is digested is discussed in the following sections.

Carbohydrates

The digestion of carbohydrates begins in the mouth. The salivary enzyme amylase begins the breakdown of food starches into maltose, a disaccharide. As the bolus of food travels through the esophagus to the stomach, no significant digestion of carbohydrates takes place. The esophagus produces no digestive enzymes but does produce mucous for lubrication. The acidic environment in the stomach stops the action of the amylase enzyme.

The next step of carbohydrate digestion takes place in the duodenum. Recall that the chyme from the stomach enters the duodenum and mixes with the digestive secretion from the pancreas, liver, and gallbladder. Pancreatic juices also contain amylase, which continues the breakdown of starch and glycogen into maltose, a disaccharide. The disaccharides are broken down into

monosaccharides by enzymes called **maltases**, **sucrases**, and **lactases**, which are also present in the brush border of the small intestinal wall. Maltase breaks down maltose into glucose. Other disaccharides, such as sucrose and lactose are broken down by sucrase and lactase, respectively. Sucrase breaks down sucrose (or "table sugar") into glucose and fructose, and lactase breaks down lactose (or "milk sugar") into glucose and galactose. The monosaccharides (glucose) thus produced are absorbed and then can be used in metabolic pathways to harness energy. The monosaccharides are transported across the intestinal epithelium into the bloodstream to be transported to the different cells in the body. The steps in carbohydrate digestion are summarized in [link] and [link].
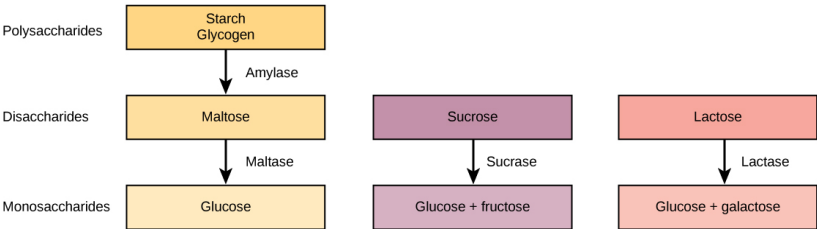
Digestion of carbohydrates is performed by several enzymes. Starch and glycogen are broken down into glucose by amylase and maltase. Sucrose (table sugar) and lactose (milk sugar) are broken down by sucrase and lactase, respectively.

Digestion of Carbohydrates				
Enzyme	**Produced By**	**Site of Action**	**Substrate Acting On**	**End Products**
Salivary amylase	Salivary glands	Mouth	Polysaccharides (Starch)	Disaccharides (maltose), oligosaccharides
Pancreatic amylase	Pancreas	Small intestine	Polysaccharides (starch)	Disaccharides (maltose), monosaccharides

Digestion of Carbohydrates				
Enzyme	**Produced By**	**Site of Action**	**Substrate Acting On**	**End Products**
Oligosaccharidases	Lining of the intestine; brush border membrane	Small intestine	Disaccharides	Monosaccharides (e.g., glucose, fructose, galactose)

Protein

A large part of protein digestion takes place in the stomach. The enzyme pepsin plays an important role in the digestion of proteins by breaking down the intact protein to peptides, which are short chains of four to nine amino acids. In the duodenum, other enzymes—**trypsin**, **elastase**, and **chymotrypsin**—act on the peptides reducing them to smaller peptides. Trypsin elastase, carboxypeptidase, and chymotrypsin are produced by the pancreas and released into the duodenum where they act on the chyme. Further breakdown of peptides to single amino acids is aided by enzymes called peptidases (those that break down peptides). Specifically, **carboxypeptidase**, **dipeptidase**, and **aminopeptidase** play important roles in reducing the peptides to free amino acids. The amino acids are absorbed into the bloodstream through the small intestines. The steps in protein digestion are summarized in [link] and [link].
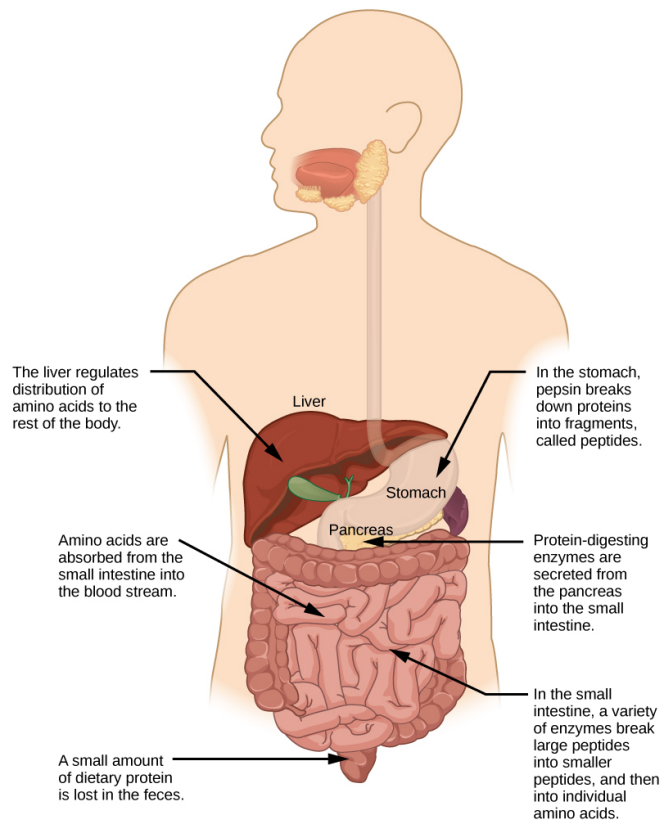
Protein digestion is a multistep process that begins in the stomach and continues through the intestines.

Digestion of Protein				
Enzyme	**Produced By**	**Site of Action**	**Substrate Acting On**	**End Products**
Pepsin	Stomach chief cells	Stomach	Proteins	Peptides
Trypsin Elastase Chymotrypsin	Pancreas	Small intestine	Proteins	Peptides

Digestion of Protein				
Enzyme	Produced By	Site of Action	Substrate Acting On	End Products
Carboxypeptidase	Pancreas	Small intestine	Peptides	Amino acids and peptides
Aminopeptidase Dipeptidase	Lining of intestine	Small intestine	Peptides	Amino acids

Lipids

Lipid digestion begins in the stomach with the aid of lingual lipase and gastric lipase. However, the bulk of lipid digestion occurs in the small intestine due to pancreatic lipase. When chyme enters the duodenum, the hormonal responses trigger the release of bile, which is produced in the liver and stored in the gallbladder. Bile aids in the digestion of lipids, primarily triglycerides by emulsification. Emulsification is a process in which large lipid globules are broken down into several small lipid globules. These small globules are more widely distributed in the chyme rather than forming large aggregates. Lipids are hydrophobic substances: in the presence of water, they will aggregate to form globules to minimize exposure to water. Bile contains bile salts, which are amphipathic, meaning they contain hydrophobic and hydrophilic parts. Thus, the bile salts hydrophilic side can interface with water on one side and the hydrophobic side interfaces with lipids on the other. By doing so, bile salts emulsify large lipid globules into small lipid globules.

Why is emulsification important for digestion of lipids? Pancreatic juices contain enzymes called lipases (enzymes that break down lipids). If the lipid in the chyme aggregates into large globules, very little surface area of the lipids is available for the lipases to act on, leaving lipid digestion incomplete. By forming an emulsion, bile salts increase the available surface area of the lipids many fold. The pancreatic lipases can then act on the lipids more efficiently and digest them, as detailed in [link]. Lipases break down the lipids into fatty acids and glycerides. These molecules can pass through the plasma membrane of the cell and enter the epithelial cells of the intestinal lining. The bile salts surround long-chain fatty acids and monoglycerides forming tiny spheres called micelles. The micelles move into the brush border of the small intestine absorptive cells where the long-chain fatty acids and monoglycerides diffuse out of the micelles into the absorptive cells leaving the micelles behind in the chyme. The long-chain fatty acids and monoglycerides recombine in the absorptive cells to form triglycerides, which aggregate into globules and become coated with proteins. These large spheres are called **chylomicrons**. Chylomicrons contain triglycerides, cholesterol, and other lipids and have proteins on their surface. The surface is also composed of the hydrophilic phosphate "heads" of phospholipids. Together, they enable the chylomicron to move in an aqueous environment without exposing the lipids to water. Chylomicrons leave the absorptive cells via exocytosis. Chylomicrons enter the lymphatic vessels, and then enter the blood in the subclavian vein.

Lipids are digested and absorbed in the small intestine.

Vitamins

Vitamins can be either water-soluble or lipid-soluble. Fat soluble vitamins are absorbed in the same manner as lipids. It is important to consume some amount of dietary lipid to aid the absorption of lipid-soluble vitamins. Water-soluble vitamins can be directly absorbed into the bloodstream from the intestine.

> **Note:**
> Link to Learning
>
>
>
> This website has an overview of the digestion of protein, fat, and carbohydrates.

- Mechanical digestion (chewing and swallowing)
- Chemical digestion of carbohydrates

- Mechanical digestion (peristaltic mixing and propulsion)
- Chemical digestion of proteins
- Absorption of lipid-soluble substances, such as aspirin

Esophagus

Liver

Gallbladder

Pylorus

Pancreas

- Mechanical digestion (mixing and propulsion, primarily by segmentation)
- Chemical digestion of carbohydrates, lipids, proteins, and nucleic acids
- Absorption of peptides, amino acids, glucose, fructose, lipids, water, minerals, and vitamins

- Mechanical digestion (segmental mixing, mass movement for propulsion)
- No chemical digestion except by bacteria
- Absorption of ions, water, minerals, vitamins, and small organic molecules produced by bacteria

Rectum

Anal sphincters

Mechanical and chemical digestion of food takes place in many steps, beginning in the mouth and ending in the rectum.

Which of the following statements about digestive processes is true?

a. Amylase, maltase, and lactase in the mouth digest carbohydrates.
b. Trypsin and lipase in the stomach digest protein.
c. Bile emulsifies lipids in the small intestine.
d. No food is absorbed until the small intestine.

Elimination

The final step in digestion is the elimination of undigested food content and waste products. The undigested food material enters the colon, where most of the water is reabsorbed. Recall that the colon is also home to the microflora called "intestinal flora" that aid in the digestion process. The semi-solid waste is moved through the colon by peristaltic movements of the muscle and is stored in the rectum. As the rectum expands in response to storage of fecal matter, it triggers the neural signals required to set up the urge to eliminate. The solid waste is eliminated through the anus using peristaltic movements of the rectum.

Common Problems with Elimination

Diarrhea and constipation are some of the most common health concerns that affect digestion. Constipation is a condition where the feces are hardened because of excess water removal in the colon. In contrast, if enough water is not removed from the feces, it results in diarrhea. Many bacteria, including the ones that cause cholera, affect the proteins involved in water reabsorption in the colon and result in excessive diarrhea.

Emesis

Emesis, or vomiting, is elimination of food by forceful expulsion through the mouth. It is often in response to an irritant that affects the digestive tract, including but not limited to viruses, bacteria, emotions, sights, and food poisoning. This forceful expulsion of the food is due to the strong contractions produced by the stomach muscles. The process of emesis is regulated by the medulla.

Section Summary

Digestion begins with ingestion, where the food is taken in the mouth. Digestion and absorption take place in a series of steps with special enzymes playing important roles in digesting carbohydrates, proteins, and lipids. Elimination describes removal of undigested food contents and waste products from the body. While most absorption occurs in the small intestines, the large intestine is responsible for the final removal of water that remains after the absorptive process of the small intestines. The cells that line the large intestine absorb some vitamins as well as any leftover salts and water. The large intestine (colon) is also where feces is formed.

Art Connections

Exercise:

Problem: [link] Which of the following statements about digestive processes is true?

    a. Amylase, maltase and lactase in the mouth digest carbohydrates.
    b. Trypsin and lipase in the stomach digest protein.
    c. Bile emulsifies lipids in the small intestine.
    d. No food is absorbed until the small intestine.

Solution:

[link] C

Review Questions

Exercise:

Problem: Where does the majority of protein digestion take place?

    a. stomach
    b. duodenum
    c. mouth
    d. jejunum

Solution:

A

Exercise:

Problem: Lipases are enzymes that break down _____.

    a. disaccharides
    b. lipids
    c. proteins
    d. cellulose

Solution:

B

Free Response

Exercise:

Problem: Explain why some dietary lipid is a necessary part of a balanced diet.

Solution:

Lipids add flavor to food and promote a sense of satiety or fullness. Fatty foods are sources of high energy; one gram of lipid contains nine calories. Lipids are also required in the diet to aid the absorption of lipid-soluble vitamins and for the production of lipid-soluble hormones.

Glossary

aminopeptidase
    protease that breaks down peptides to single amino acids; secreted by the brush border of small intestine

carboxypeptidase

protease that breaks down peptides to single amino acids; secreted by the brush border of the small intestine

chylomicron
small lipid globule

chymotrypsin
pancreatic protease

digestion
mechanical and chemical break down of food into small organic fragments

dipeptidase
protease that breaks down peptides to single amino acids; secreted by the brush border of small intestine

elastase
pancreatic protease

ingestion
act of taking in food

lactase
enzyme that breaks down lactose into glucose and galactose

maltase
enzyme that breaks down maltose into glucose

sucrase
enzyme that breaks down sucrose into glucose and fructose

trypsin
pancreatic protease that breaks down protein

Digestive System Regulation
By the end of this section, you will be able to:

- Discuss the role of neural regulation in digestive processes
- Explain how hormones regulate digestion

The brain is the control center for the sensation of hunger and satiety. The functions of the digestive system are regulated through neural and hormonal responses.

Neural Responses to Food

In reaction to the smell, sight, or thought of food, like that shown in [link], the first response is that of salivation. The salivary glands secrete more saliva in response to stimulation by the autonomic nervous system triggered by food in preparation for digestion. Simultaneously, the stomach begins to produce hydrochloric acid to digest the food. Recall that the peristaltic movements of the esophagus and other organs of the digestive tract are under the control of the brain. The brain prepares these muscles for movement as well. When the stomach is full, the part of the brain that detects satiety signals fullness. There are three overlapping phases of gastric control—the cephalic phase, the gastric phase, and the intestinal phase—each requires many enzymes and is under neural control as well.

Seeing a plate of food triggers the secretion of saliva in the mouth and the production of HCL in the stomach. (credit: Kelly Bailey)

Digestive Phases

The response to food begins even before food enters the mouth. The first phase of ingestion, called the **cephalic phase**, is controlled by the neural response to the stimulus provided by food. All aspects—such as sight, sense, and smell—trigger the neural responses resulting in salivation and secretion of gastric juices. The gastric and salivary secretion in the cephalic phase can also take place due to the thought of food. Right now, if you think about a piece of chocolate or a crispy potato chip, the increase in salivation is a cephalic phase response to the thought. The central nervous system prepares the stomach to receive food.

The **gastric phase** begins once the food arrives in the stomach. It builds on the stimulation provided during the cephalic phase. Gastric acids and enzymes process the ingested materials. The gastric phase is stimulated by

(1) distension of the stomach, (2) a decrease in the pH of the gastric contents, and (3) the presence of undigested material. This phase consists of local, hormonal, and neural responses. These responses stimulate secretions and powerful contractions.

The **intestinal phase** begins when chyme enters the small intestine triggering digestive secretions. This phase controls the rate of gastric emptying. In addition to gastrin emptying, when chyme enters the small intestine, it triggers other hormonal and neural events that coordinate the activities of the intestinal tract, pancreas, liver, and gallbladder.

Hormonal Responses to Food

The **endocrine system** controls the response of the various glands in the body and the release of hormones at the appropriate times.

One of the important factors under hormonal control is the stomach acid environment. During the gastric phase, the hormone **gastrin** is secreted by G cells in the stomach in response to the presence of proteins. Gastrin stimulates the release of stomach acid, or hydrochloric acid (HCl) which aids in the digestion of the proteins. However, when the stomach is emptied, the acidic environment need not be maintained and a hormone called **somatostatin** stops the release of hydrochloric acid. This is controlled by a negative feedback mechanism.

In the duodenum, digestive secretions from the liver, pancreas, and gallbladder play an important role in digesting chyme during the intestinal phase. In order to neutralize the acidic chyme, a hormone called **secretin** stimulates the pancreas to produce alkaline bicarbonate solution and deliver it to the duodenum. Secretin acts in tandem with another hormone called **cholecystokinin** (CCK). Not only does CCK stimulate the pancreas to produce the requisite pancreatic juices, it also stimulates the gallbladder to release bile into the duodenum.

Note:

Another level of hormonal control occurs in response to the composition of food. Foods high in lipids take a long time to digest. A hormone called **gastric inhibitory peptide** is secreted by the small intestine to slow down the peristaltic movements of the intestine to allow fatty foods more time to be digested and absorbed.

Understanding the hormonal control of the digestive system is an important area of ongoing research. Scientists are exploring the role of each hormone in the digestive process and developing ways to target these hormones. Advances could lead to knowledge that may help to battle the obesity epidemic.

Section Summary

The brain and the endocrine system control digestive processes. The brain controls the responses of hunger and satiety. The endocrine system controls the release of hormones and enzymes required for digestion of food in the digestive tract.

Review Questions

Exercise:

Problem:

Which hormone controls the release of bile from the gallbladder

    a. pepsin
    b. amylase
    c. CCK
    d. gastrin

Solution:

C

Exercise:

Problem: Which hormone stops acid secretion in the stomach?

    a. gastrin
    b. somatostatin
    c. gastric inhibitory peptide
    d. CCK

Solution:

B

Free Response

Exercise:

Problem: Describe how hormones regulate digestion.

Solution:

Hormones control the different digestive enzymes that are secreted in the stomach and the intestine during the process of digestion and absorption. For example, the hormone gastrin stimulates stomach acid secretion in response to food intake. The hormone somatostatin stops the release of stomach acid.

Exercise:

Problem:

Describe one or more scenarios where loss of hormonal regulation of digestion can lead to diseases.

Solution:

There are many cases where loss of hormonal regulation can lead to illnesses. For example, the bilirubin produced by the breakdown of red blood cells is converted to bile by the liver. When there is malfunction of this process, there is excess bilirubin in the blood and bile levels are low. As a result, the body struggles with dealing with fatty food. This is why a patient suffering from jaundice is asked to eat a diet with almost zero fat.

Glossary

cephalic phase
    first phase of digestion, controlled by the neural response to the stimulus provided by food

cholecystokinin
    hormone that stimulates the contraction of the gallbladder to release bile

endocrine system
    system that controls the response of the various glands in the body and the release of hormones at the appropriate times

gastric inhibitory peptide

hormone secreted by the small intestine in the presence of fatty acids and sugars; it also inhibits acid production and peristalsis in order to slow down the rate at which food enters the small intestine

gastric phase
digestive phase beginning once food enters the stomach; gastric acids and enzymes process the ingested materials

gastrin
hormone which stimulates hydrochloric acid secretion in the stomach

intestinal phase
third digestive phase; begins when chyme enters the small intestine triggering digestive secretions and controlling the rate of gastric emptying

secretin
hormone which stimulates sodium bicarbonate secretion in the small intestine

somatostatin
hormone released to stop acid secretion when the stomach is empty

Introduction
class="introduction"

Just as highway systems transport people and goods through a complex network, the circulatory system transports nutrients, gases, and wastes throughout the animal body. (credit: modification of work by Andrey Belenko)

Most animals are complex multicellular organisms that require a mechanism for transporting nutrients throughout their bodies and removing waste products. The circulatory system has evolved over time from simple diffusion through cells in the early evolution of animals to a complex network of blood vessels that reach all parts of the human body. This extensive network supplies the cells, tissues, and organs with oxygen and nutrients, and removes carbon dioxide and waste, which are byproducts of respiration.

At the core of the human circulatory system is the heart. The size of a clenched fist, the human heart is protected beneath the rib cage. Made of specialized and unique cardiac muscle, it pumps blood throughout the body and to the heart itself. Heart contractions are driven by intrinsic electrical impulses that the brain and endocrine hormones help to regulate. Understanding the heart's basic anatomy and function is important to understanding the body's circulatory and respiratory systems.

Gas exchange is one essential function of the circulatory system. A circulatory system is not needed in organisms with no specialized respiratory organs because oxygen and carbon dioxide diffuse directly between their body tissues and the external environment. However, in organisms that possess lungs and gills, oxygen must be transported from these specialized respiratory organs to the body tissues via a circulatory

system. Therefore, circulatory systems have had to evolve to accommodate the great diversity of body sizes and body types present among animals.

Overview of the Circulatory System
By the end of this section, you will be able to:

- Describe an open and closed circulatory system
- Describe interstitial fluid and hemolymph
- Compare and contrast the organization and evolution of the vertebrate circulatory system.

In all animals, except a few simple types, the circulatory system is used to transport nutrients and gases through the body. Simple diffusion allows some water, nutrient, waste, and gas exchange into primitive animals that are only a few cell layers thick; however, bulk flow is the only method by which the entire body of larger more complex organisms is accessed.

Circulatory System Architecture

The circulatory system is effectively a network of cylindrical vessels: the arteries, veins, and capillaries that emanate from a pump, the heart. In all vertebrate organisms, as well as some invertebrates, this is a closed-loop system, in which the blood is not free in a cavity. In a **closed circulatory system**, blood is contained inside blood vessels and circulates **unidirectionally** from the heart around the systemic circulatory route, then returns to the heart again, as illustrated in [link]**a**. As opposed to a closed system, arthropods—including insects, crustaceans, and most mollusks— have an open circulatory system, as illustrated in [link]**b**. In an **open circulatory system**, the blood is not enclosed in the blood vessels but is pumped into a cavity called a **hemocoel** and is called **hemolymph** because the blood mixes with the **interstitial fluid**. As the heart beats and the animal moves, the hemolymph circulates around the organs within the body cavity and then reenters the hearts through openings called **ostia**. This movement allows for gas and nutrient exchange. An open circulatory system does not use as much energy as a closed system to operate or to maintain; however, there is a trade-off with the amount of blood that can be moved to metabolically active organs and tissues that require high levels of oxygen. In fact, one reason that insects with wing spans of up to two feet wide (70 cm) are not around today is probably because they were outcompeted by the arrival of birds 150 million years ago. Birds, having a

closed circulatory system, are thought to have moved more agilely, allowing them to get food faster and possibly to prey on the insects.
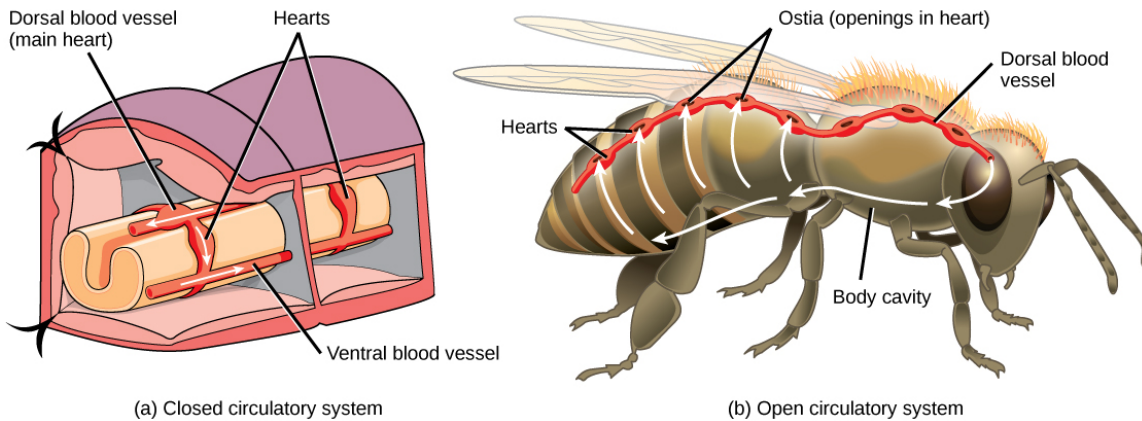
In (a) closed circulatory systems, the heart pumps blood through vessels that are separate from the interstitial fluid of the body. Most vertebrates and some invertebrates, like this annelid earthworm, have a closed circulatory system. In (b) open circulatory systems, a fluid called hemolymph is pumped through a blood vessel that empties into the body cavity. Hemolymph returns to the blood vessel through openings called ostia. Arthropods like this bee and most mollusks have open circulatory systems.

Circulatory System Variation in Animals

The circulatory system varies from simple systems in invertebrates to more complex systems in vertebrates. The simplest animals, such as the sponges (Porifera) and rotifers (Rotifera), do not need a circulatory system because diffusion allows adequate exchange of water, nutrients, and waste, as well as dissolved gases, as shown in [link]**a**. Organisms that are more complex but still only have two layers of cells in their body plan, such as jellies (Cnidaria) and comb jellies (Ctenophora) also use diffusion through their epidermis and internally through the gastrovascular compartment. Both

their internal and external tissues are bathed in an aqueous environment and exchange fluids by diffusion on both sides, as illustrated in [link]**b**. Exchange of fluids is assisted by the pulsing of the jellyfish body.
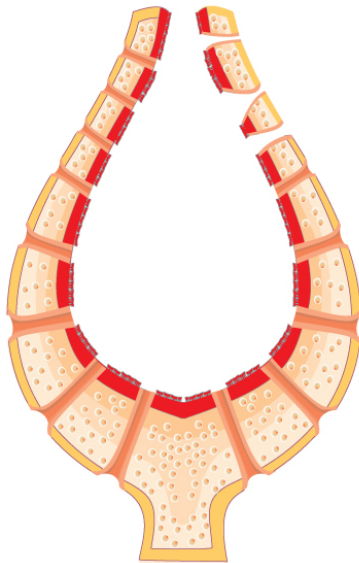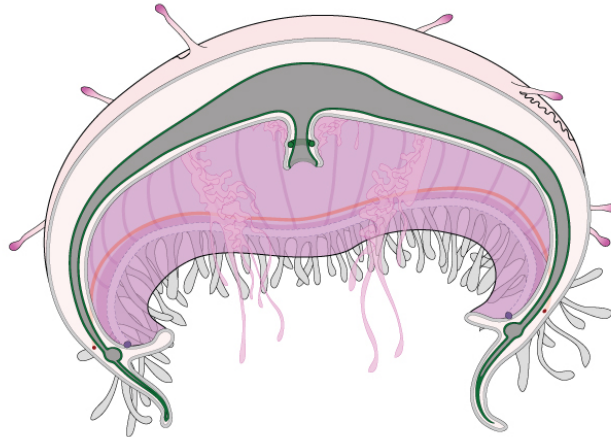
(a) Sponge   (b) Jellyfish

Simple animals consisting of a single cell layer such as the (a) sponge or only a few cell layers such as the (b) jellyfish do not have a circulatory system. Instead, gases, nutrients, and wastes are exchanged by diffusion.

For more complex organisms, diffusion is not efficient for cycling gases, nutrients, and waste effectively through the body; therefore, more complex circulatory systems evolved. Most arthropods and many mollusks have open circulatory systems. In an open system, an elongated beating heart pushes the hemolymph through the body and muscle contractions help to move fluids. The larger more complex crustaceans, including lobsters, have developed arterial-like vessels to push blood through their bodies, and the most active mollusks, such as squids, have evolved a closed circulatory system and are able to move rapidly to catch prey. Closed circulatory systems are a characteristic of vertebrates; however, there are significant

differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptation during evolution and associated differences in anatomy. [link] illustrates the basic circulatory systems of some vertebrates: fish, amphibians, reptiles, and mammals.

(a) Fish

(b) Amphibians

(c) Reptile

(d) Mammals
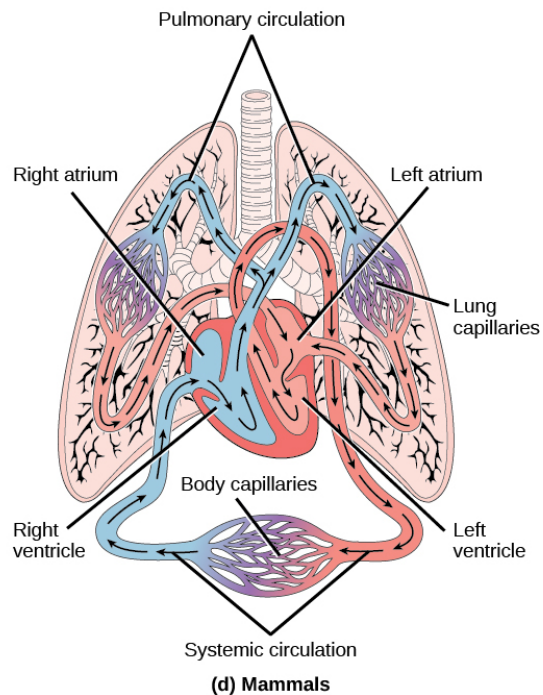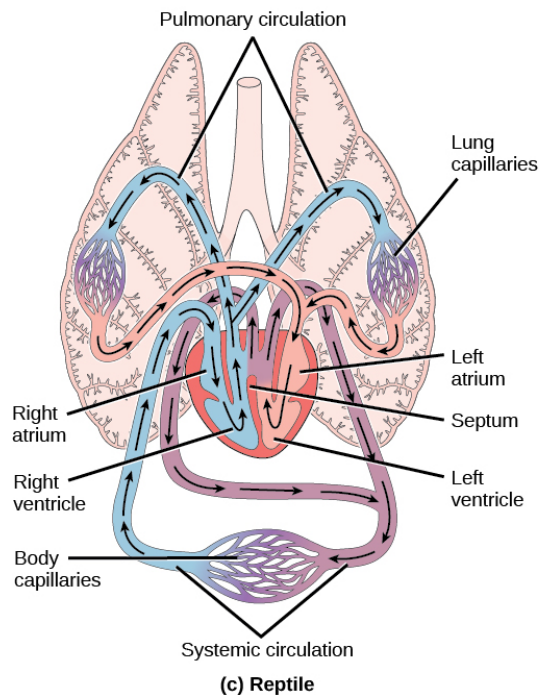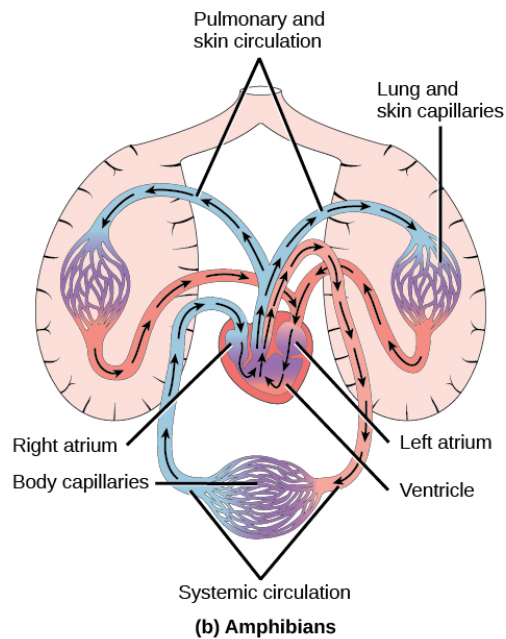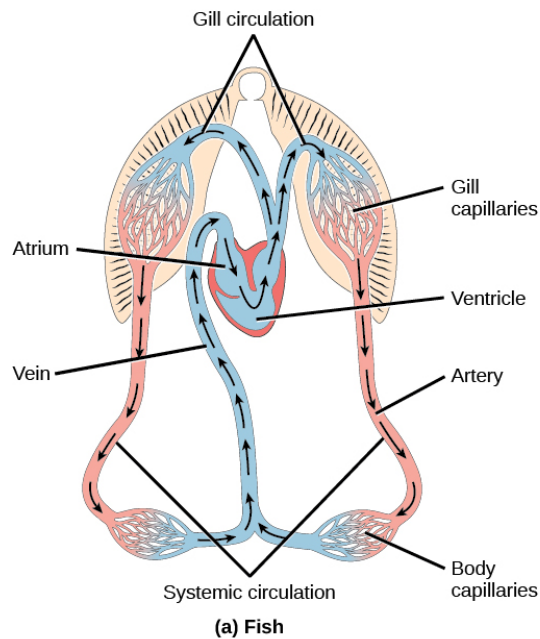
(a) Fish have the simplest circulatory systems of the vertebrates: blood flows unidirectionally from the two-chambered heart through the gills and then the rest of the body. (b) Amphibians have two circulatory routes: one for oxygenation of the blood through the lungs and skin, and the other to take oxygen to the rest of the body. The blood is pumped from a three-chambered heart with two atria and a single ventricle. (c) Reptiles also have two circulatory routes; however, blood is only oxygenated through the lungs. The heart is three chambered, but the ventricles are partially separated so some mixing of oxygenated and deoxygenated blood occurs except in crocodilians and birds. (d) Mammals and birds have the most efficient heart with four chambers that completely separate the oxygenated and deoxygenated blood; it pumps only oxygenated blood through the body and deoxygenated blood to the lungs.

As illustrated in [link]**a** Fish have a single circuit for blood flow and a two-chambered heart that has only a single atrium and a single ventricle. The atrium collects blood that has returned from the body and the ventricle pumps the blood to the gills where gas exchange occurs and the blood is re-oxygenated; this is called **gill circulation**. The blood then continues through the rest of the body before arriving back at the atrium; this is called **systemic circulation**. This unidirectional flow of blood produces a gradient of oxygenated to deoxygenated blood around the fish's systemic circuit. The result is a limit in the amount of oxygen that can reach some of the organs and tissues of the body, reducing the overall metabolic capacity of fish.

In amphibians, reptiles, birds, and mammals, blood flow is directed in two circuits: one through the lungs and back to the heart, which is called **pulmonary circulation**, and the other throughout the rest of the body and its organs including the brain (systemic circulation). In amphibians, gas exchange also occurs through the skin during pulmonary circulation and is referred to as **pulmocutaneous circulation**.

As shown in [link]**b**, amphibians have a three-chambered heart that has two atria and one ventricle rather than the two-chambered heart of fish. The two **atria** (superior heart chambers) receive blood from the two different circuits (the lungs and the systems), and then there is some mixing of the blood in the heart's **ventricle** (inferior heart chamber), which reduces the efficiency of oxygenation. The advantage to this arrangement is that high pressure in the vessels pushes blood to the lungs and body. The mixing is mitigated by a ridge within the ventricle that diverts oxygen-rich blood through the systemic circulatory system and deoxygenated blood to the pulmocutaneous circuit. For this reason, amphibians are often described as having **double circulation**.

Most reptiles also have a three-chambered heart similar to the amphibian heart that directs blood to the pulmonary and systemic circuits, as shown in [link]**c**. The ventricle is divided more effectively by a partial septum, which results in less mixing of oxygenated and deoxygenated blood. Some reptiles (alligators and crocodiles) are the most primitive animals to exhibit a four-chambered heart. Crocodilians have a unique circulatory mechanism where the heart shunts blood from the lungs toward the stomach and other organs during long periods of submergence, for instance, while the animal waits for prey or stays underwater waiting for prey to rot. One adaptation includes two main arteries that leave the same part of the heart: one takes blood to the lungs and the other provides an alternate route to the stomach and other parts of the body. Two other adaptations include a hole in the heart between the two ventricles, called the foramen of Panizza, which allows blood to move from one side of the heart to the other, and specialized connective tissue that slows the blood flow to the lungs. Together these adaptations have made crocodiles and alligators one of the most evolutionarily successful animal groups on earth.

In mammals and birds, the heart is also divided into four chambers: two atria and two ventricles, as illustrated in [link]**d**. The oxygenated blood is separated from the deoxygenated blood, which improves the efficiency of double circulation and is probably required for the warm-blooded lifestyle of mammals and birds. The four-chambered heart of birds and mammals evolved independently from a three-chambered heart. The independent

evolution of the same or a similar biological trait is referred to as convergent evolution.

Section Summary

In most animals, the circulatory system is used to transport blood through the body. Some primitive animals use diffusion for the exchange of water, nutrients, and gases. However, complex organisms use the circulatory system to carry gases, nutrients, and waste through the body. Circulatory systems may be open (mixed with the interstitial fluid) or closed (separated from the interstitial fluid). Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptions during evolution and associated differences in anatomy. Fish have a two-chambered heart with unidirectional circulation. Amphibians have a three-chambered heart, which has some mixing of the blood, and they have double circulation. Most non-avian reptiles have a three-chambered heart, but have little mixing of the blood; they have double circulation. Mammals and birds have a four-chambered heart with no mixing of the blood and double circulation.

Review Questions

Exercise:

  Problem:

  Why are open circulatory systems advantageous to some animals?

      a. They use less metabolic energy.
      b. They help the animal move faster.
      c. They do not need a heart.
      d. They help large insects develop.

  Solution:

A

Exercise:

Problem:

Some animals use diffusion instead of a circulatory system. Examples include:

    a. birds and jellyfish
    b. flatworms and arthropods
    c. mollusks and jellyfish
    d. None of the above

Solution:

D

Exercise:

Problem:

Blood flow that is directed through the lungs and back to the heart is called _____.

    a. unidirectional circulation
    b. gill circulation
    c. pulmonary circulation
    d. pulmocutaneous circulation

Solution:

C

Free Response

Exercise:

Problem: Describe a closed circulatory system.

Solution:

A closed circulatory system is a closed-loop system, in which blood is not free in a cavity. Blood is separate from the bodily interstitial fluid and contained within blood vessels. In this type of system, blood circulates unidirectionally from the heart around the systemic circulatory route, and then returns to the heart.

Exercise:

Problem: Describe systemic circulation.

Solution:

Systemic circulation flows through the systems of the body. The blood flows away from the heart to the brain, liver, kidneys, stomach, and other organs, the limbs, and the muscles of the body; it then returns to the heart.

Glossary

atrium
> (plural: atria) chamber of the heart that receives blood from the veins and sends blood to the ventricles

closed circulatory system
> system in which the blood is separated from the bodily interstitial fluid and contained in blood vessels

double circulation
> flow of blood in two circuits: the pulmonary circuit through the lungs and the systemic circuit through the organs and body

gill circulation

circulatory system that is specific to animals with gills for gas exchange; the blood flows through the gills for oxygenation

hemocoel
cavity into which blood is pumped in an open circulatory system

hemolymph
mixture of blood and interstitial fluid that is found in insects and other arthropods as well as most mollusks

interstitial fluid
fluid between cells

open circulatory system
system in which the blood is mixed with interstitial fluid and directly covers the organs

ostium
(plural: ostia) holes between blood vessels that allow the movement of hemolymph through the body of insects, arthropods, and mollusks with open circulatory systems

pulmocutaneous circulation
circulatory system in amphibians; the flow of blood to the lungs and the moist skin for gas exchange

pulmonary circulation
flow of blood away from the heart through the lungs where oxygenation occurs and then returns to the heart again

systemic circulation
flow of blood away from the heart to the brain, liver, kidneys, stomach, and other organs, the limbs, and the muscles of the body, and then the return of this blood to the heart

unidirectional circulation
flow of blood in a single circuit; occurs in fish where the blood flows through the gills, then past the organs and the rest of the body, before

returning to the heart

ventricle
(heart) large inferior chamber of the heart that pumps blood into
arteries

Components of the Blood
By the end of this section, you will be able to:

- List the basic components of the blood
- Compare red and white blood cells
- Describe blood plasma and serum

Hemoglobin is responsible for distributing oxygen, and to a lesser extent, carbon dioxide, throughout the circulatory systems of humans, vertebrates, and many invertebrates. The blood is more than the proteins, though. Blood is actually a term used to describe the liquid that moves through the vessels and includes **plasma** (the liquid portion, which contains water, proteins, salts, lipids, and glucose) and the cells (red and white cells) and cell fragments called **platelets**. Blood plasma is actually the dominant component of blood and contains the water, proteins, electrolytes, lipids, and glucose. The cells are responsible for carrying the gases (red cells) and immune the response (white). The platelets are responsible for blood clotting. Interstitial fluid that surrounds cells is separate from the blood, but in hemolymph, they are combined. In humans, cellular components make up approximately 45 percent of the blood and the liquid plasma 55 percent. Blood is 20 percent of a person's extracellular fluid and eight percent of weight.

The Role of Blood in the Body

Blood, like the human blood illustrated in [link] is important for regulation of the body's systems and homeostasis. Blood helps maintain homeostasis by stabilizing pH, temperature, osmotic pressure, and by eliminating excess heat. Blood supports growth by distributing nutrients and hormones, and by removing waste. Blood plays a protective role by transporting clotting factors and platelets to prevent blood loss and transporting the disease-fighting agents or **white blood cells** to sites of infection.
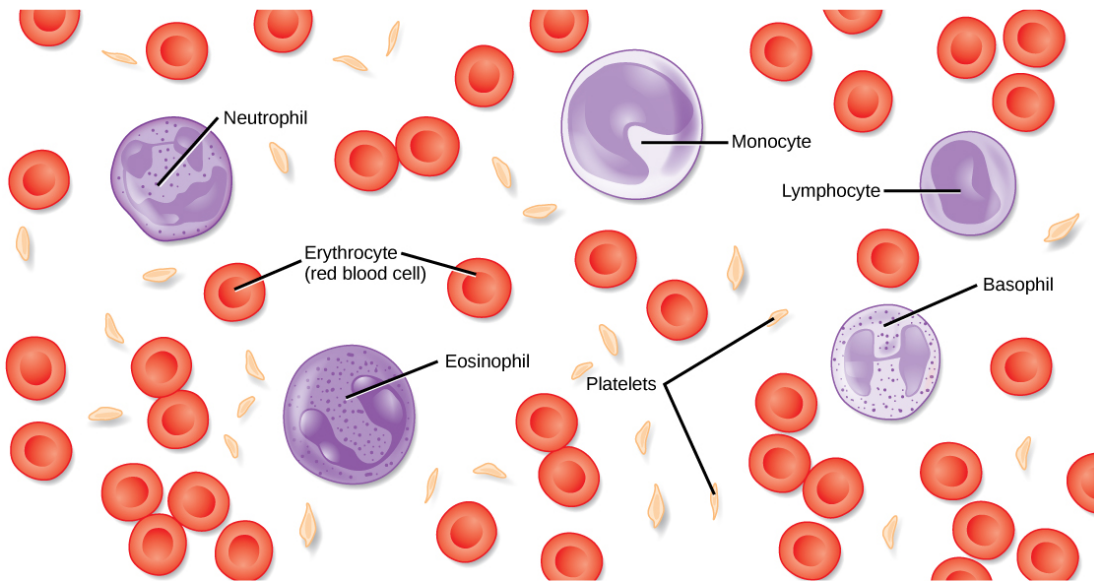
The cells and cellular components of human blood are shown. Red blood cells deliver oxygen to the cells and remove carbon dioxide. White blood cells—including neutrophils, monocytes, lymphocytes, eosinophils, and basophils—are involved in the immune response. Platelets form clots that prevent blood loss after injury.

Red Blood Cells

Red blood cells, or erythrocytes (erythro- = "red"; -cyte = "cell"), are specialized cells that circulate through the body delivering oxygen to cells; they are formed from stem cells in the bone marrow. In mammals, red blood cells are small biconcave cells that at maturity do not contain a nucleus or mitochondria and are only 7–8 µm in size. In birds and non-avian reptiles, a nucleus is still maintained in red blood cells.

The red coloring of blood comes from the iron-containing protein hemoglobin, illustrated in [link]**a**. The principal job of this protein is to carry oxygen, but it also transports carbon dioxide as well. Hemoglobin is packed into red blood cells at a rate of about 250 million molecules of hemoglobin per cell. Each hemoglobin molecule binds four oxygen

molecules so that each red blood cell carries one billion molecules of oxygen. There are approximately 25 trillion red blood cells in the five liters of blood in the human body, which could carry up to 25 sextillion (25 × 10^{21}) molecules of oxygen in the body at any time. In mammals, the lack of organelles in erythrocytes leaves more room for the hemoglobin molecules, and the lack of mitochondria also prevents use of the oxygen for metabolic respiration. Only mammals have anucleated red blood cells, and some mammals (camels, for instance) even have nucleated red blood cells. The advantage of nucleated red blood cells is that these cells can undergo mitosis. Anucleated red blood cells metabolize anaerobically (without oxygen), making use of a primitive metabolic pathway to produce ATP and increase the efficiency of oxygen transport.

Not all organisms use hemoglobin as the method of oxygen transport. Invertebrates that utilize hemolymph rather than blood use different pigments to bind to the oxygen. These pigments use copper or iron to the oxygen. Invertebrates have a variety of other respiratory pigments. Hemocyanin, a blue-green, copper-containing protein, illustrated in [link]**b** is found in mollusks, crustaceans, and some of the arthropods. Chlorocruorin, a green-colored, iron-containing pigment is found in four families of polychaete tubeworms. Hemerythrin, a red, iron-containing protein is found in some polychaete worms and annelids and is illustrated in [link]**c**. Despite the name, hemerythrin does not contain a heme group and its oxygen-carrying capacity is poor compared to hemoglobin.

(a) Hemoglobin   (b) Hemocyanin   (c) Hemerythrin
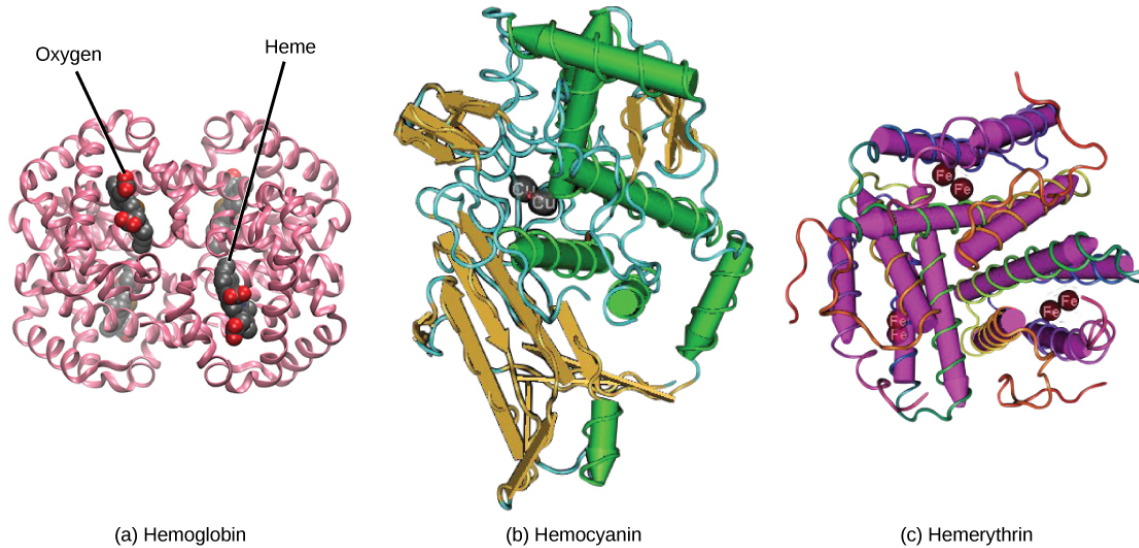
In most vertebrates, (a) hemoglobin delivers oxygen to the body and removes some carbon dioxide. Hemoglobin is composed of four protein subunits, two alpha chains and two beta chains, and a heme group that has iron associated with it. The iron reversibly associates with oxygen, and in so doing is oxidized from Fe^{2+} to Fe^{3+}. In most mollusks and some arthropods, (b) hemocyanin delivers oxygen. Unlike hemoglobin, hemolymph is not carried in blood cells, but floats free in the hemolymph. Copper instead of iron binds the oxygen, giving the hemolymph a blue-green color. In annelids, such as the earthworm, and some other invertebrates, (c) hemerythrin carries oxygen. Like hemoglobin, hemerythrin is carried in blood cells and has iron associated with it, but despite its name, hemerythrin does not contain heme.

The small size and large surface area of red blood cells allows for rapid diffusion of oxygen and carbon dioxide across the plasma membrane. In the lungs, carbon dioxide is released and oxygen is taken in by the blood. In the tissues, oxygen is released from the blood and carbon dioxide is bound for transport back to the lungs. Studies have found that hemoglobin also binds nitrous oxide (NO). NO is a vasodilator that relaxes the blood vessels and capillaries and may help with gas exchange and the passage of red blood cells through narrow vessels. Nitroglycerin, a heart medication for angina

and heart attacks, is converted to NO to help relax the blood vessels and increase oxygen flow through the body.

A characteristic of red blood cells is their glycolipid and glycoprotein coating; these are lipids and proteins that have carbohydrate molecules attached. In humans, the surface glycoproteins and glycolipids on red blood cells vary between individuals, producing the different blood types, such as A, B, and O. Red blood cells have an average life span of 120 days, at which time they are broken down and recycled in the liver and spleen by phagocytic macrophages, a type of white blood cell.

White Blood Cells

White blood cells, also called leukocytes (leuko = white), make up approximately one percent by volume of the cells in blood. The role of white blood cells is very different than that of red blood cells: they are primarily involved in the immune response to identify and target pathogens, such as invading bacteria, viruses, and other foreign organisms. White blood cells are formed continually; some only live for hours or days, but some live for years.

The morphology of white blood cells differs significantly from red blood cells. They have nuclei and do not contain hemoglobin. The different types of white blood cells are identified by their microscopic appearance after histologic staining, and each has a different specialized function. The two main groups, both illustrated in [link] are the granulocytes, which include the neutrophils, eosinophils, and basophils, and the agranulocytes, which include the monocytes and lymphocytes.

Neutrophil Eosinophil Basophil Monocyte Lymphocyte
(a) Granulocytes (b) Agranulocytes
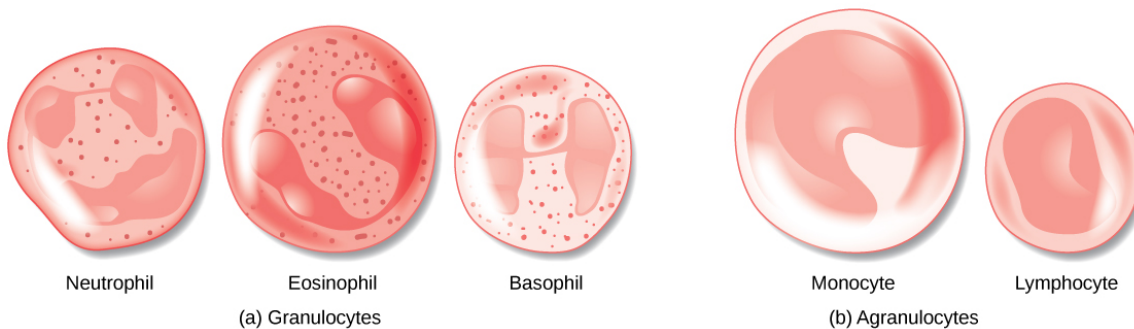
(a) Granulocytes—including neutrophils, eosinophils and basophils—are characterized by a lobed nucleus and granular inclusions in the cytoplasm. Granulocytes are typically first-responders during injury or infection. (b) Agranulocytes include lymphocytes and monocytes. Lymphocytes, including B and T cells, are responsible for adaptive immune response. Monocytes differentiate into macrophages and dendritic cells, which in turn respond to infection or injury.

Granulocytes contain granules in their cytoplasm; the agranulocytes are so named because of the lack of granules in their cytoplasm. Some leukocytes become macrophages that either stay at the same site or move through the blood stream and gather at sites of infection or inflammation where they are attracted by chemical signals from foreign particles and damaged cells. Lymphocytes are the primary cells of the immune system and include B cells, T cells, and natural killer cells. B cells destroy bacteria and inactivate their toxins. They also produce antibodies. T cells attack viruses, fungi, some bacteria, transplanted cells, and cancer cells. T cells attack viruses by releasing toxins that kill the viruses. Natural killer cells attack a variety of infectious microbes and certain tumor cells.

One reason that HIV poses significant management challenges is because the virus directly targets T cells by gaining entry through a receptor. Once inside the cell, HIV then multiplies using the T cell's own genetic machinery. After the HIV virus replicates, it is transmitted directly from the infected T cell to macrophages. The presence of HIV can remain

unrecognized for an extensive period of time before full disease symptoms develop.

Platelets and Coagulation Factors

Blood must clot to heal wounds and prevent excess blood loss. Small cell fragments called platelets (thrombocytes) are attracted to the wound site where they adhere by extending many projections and releasing their contents. These contents activate other platelets and also interact with other coagulation factors, which convert fibrinogen, a water-soluble protein present in blood serum into fibrin (a non-water soluble protein), causing the blood to clot. Many of the clotting factors require vitamin K to work, and vitamin K deficiency can lead to problems with blood clotting. Many platelets converge and stick together at the wound site forming a platelet plug (also called a fibrin clot), as illustrated in [link]**b**. The plug or clot lasts for a number of days and stops the loss of blood. Platelets are formed from the disintegration of larger cells called megakaryocytes, like that shown in [link]**a**. For each megakaryocyte, 2000–3000 platelets are formed with 150,000 to 400,000 platelets present in each cubic millimeter of blood. Each platelet is disc shaped and 2–4 µm in diameter. They contain many small vesicles but do not contain a nucleus.
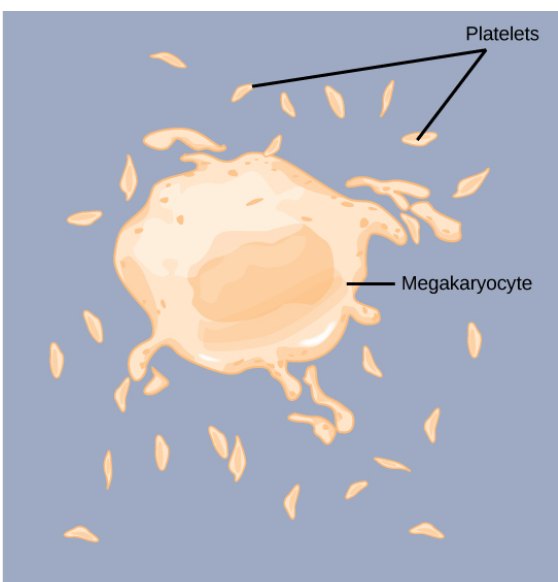
(a)
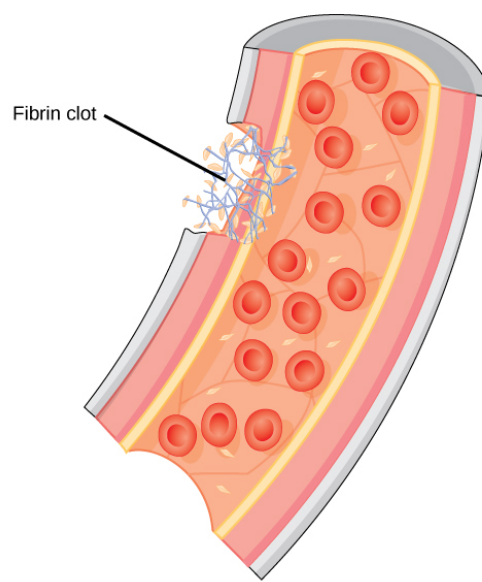
(b)

(a) Platelets are formed from large cells called megakaryocytes. The megakaryocyte breaks up into thousands of fragments that become platelets. (b) Platelets are required for clotting of the blood. The platelets collect at a wound site in conjunction with other clotting factors, such as fibrinogen, to form a fibrin clot that prevents blood loss and allows the wound to heal.

Plasma and Serum

The liquid component of blood is called plasma, and it is separated by spinning or centrifuging the blood at high rotations (3000 rpm or higher). The blood cells and platelets are separated by centrifugal forces to the bottom of a specimen tube. The upper liquid layer, the plasma, consists of 90 percent water along with various substances required for maintaining the body's pH, osmotic load, and for protecting the body. The plasma also contains the coagulation factors and antibodies.

The plasma component of blood without the coagulation factors is called the **serum**. Serum is similar to interstitial fluid in which the correct composition of key ions acting as electrolytes is essential for normal functioning of muscles and nerves. Other components in the serum include proteins that assist with maintaining pH and osmotic balance while giving viscosity to the blood. The serum also contains antibodies, specialized proteins that are important for defense against viruses and bacteria. Lipids, including cholesterol, are also transported in the serum, along with various other substances including nutrients, hormones, metabolic waste, plus external substances, such as, drugs, viruses, and bacteria.

Human serum albumin is the most abundant protein in human blood plasma and is synthesized in the liver. Albumin, which constitutes about half of the blood serum protein, transports hormones and fatty acids, buffers pH, and maintains osmotic pressures. Immunoglobin is a protein antibody produced in the mucosal lining and plays an important role in antibody mediated immunity.

Note:

Evolution Connection

Blood Types Related to Proteins on the Surface of the Red Blood Cells
Red blood cells are coated in antigens made of glycolipids and glycoproteins. The composition of these molecules is determined by genetics, which have evolved over time. In humans, the different surface antigens are grouped into 24 different blood groups with more than 100 different antigens on each red blood cell. The two most well known blood groups are the ABO, shown in [link], and Rh systems. The surface antigens in the ABO blood group are glycolipids, called antigen A and antigen B. People with blood type A have antigen A, those with blood type B have antigen B, those with blood type AB have both antigens, and people with blood type O have neither antigen. Antibodies called agglutinougens are found in the blood plasma and react with the A or B antigens, if the two are mixed. When type A and type B blood are combined, agglutination (clumping) of the blood occurs because of antibodies in the plasma that bind with the opposing antigen; this causes clots that coagulate in the kidney causing kidney failure. Type O blood has neither A or B antigens, and therefore, type O blood can be given to all blood types. Type O negative blood is the universal donor. Type AB positive blood is the universal acceptor because it has both A and B antigen. The ABO blood groups were discovered in 1900 and 1901 by Karl Landsteiner at the University of Vienna.

The Rh blood group was first discovered in Rhesus monkeys. Most people have the Rh antigen (Rh+) and do not have anti-Rh antibodies in their blood. The few people who do not have the Rh antigen and are Rh– can develop anti-Rh antibodies if exposed to Rh+ blood. This can happen after a blood transfusion or after an Rh– woman has an Rh+ baby. The first exposure does not usually cause a reaction; however, at the second exposure, enough antibodies have built up in the blood to produce a reaction that causes agglutination and breakdown of red blood cells. An injection can prevent this reaction.

(O)   (A)   (B)   (AB)
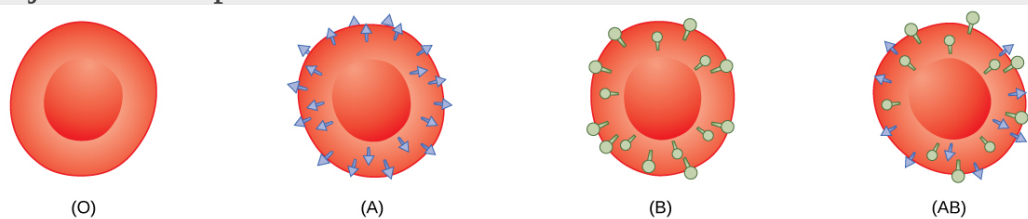
Human red blood cells may have either type A or B glycoproteins on their surface, both glycoproteins combined (AB), or neither (O). The glycoproteins serve as antigens and can elicit an immune response in a person who receives a transfusion containing unfamiliar antigens. Type O blood, which has no A or B antigens, does not elicit an immune response when injected into a person of any blood type. Thus, O is considered the universal donor. Persons with type AB blood can accept blood from any blood type, and type AB is considered the universal acceptor.

Note:
Link to Learning

Play a blood typing game on the [Nobel Prize website](#) to solidify your understanding of blood types.

Section Summary

Specific components of the blood include red blood cells, white blood cells, platelets, and the plasma, which contains coagulation factors and serum. Blood is important for regulation of the body's pH, temperature, osmotic pressure, the circulation of nutrients and removal of waste, the distribution of hormones from endocrine glands, and the elimination of excess heat; it also contains components for blood clotting. Red blood cells are specialized

cells that contain hemoglobin and circulate through the body delivering oxygen to cells. White blood cells are involved in the immune response to identify and target invading bacteria, viruses, and other foreign organisms; they also recycle waste components, such as old red blood cells. Platelets and blood clotting factors cause the change of the soluble protein fibrinogen to the insoluble protein fibrin at a wound site forming a plug. Plasma consists of 90 percent water along with various substances, such as coagulation factors and antibodies. The serum is the plasma component of the blood without the coagulation factors.

Review Questions

Exercise:

Problem: White blood cells:

a. can be classified as granulocytes or agranulocytes
b. defend the body against bacteria and viruses
c. are also called leucocytes
d. All of the above

Solution:

D

Exercise:

Problem: Platelet plug formation occurs at which point?

a. when large megakaryocytes break up into thousands of smaller fragments
b. when platelets are dispersed through the blood stream
c. when platelets are attracted to a site of blood vessel damage
d. none of the above

Solution:

C

Exercise:

Problem:

In humans, the plasma comprises what percentage of the blood?

    a. 45 percent
    b. 55 percent
    c. 25 percent
    d. 90 percent

Solution:

B

Exercise:

Problem:

The red blood cells of birds differ from mammalian red blood cells because:

    a. they are white and have nuclei
    b. they do not have nuclei
    c. they have nuclei
    d. they fight disease

Solution:

C

Free Response

Exercise:

Problem: Describe the cause of different blood type groups.

Solution:

Red blood cells are coated with proteins called antigens made of glycolipids and glycoproteins. When type A and type B blood are mixed, the blood agglutinates because of antibodies in the plasma that bind with the opposing antigen. Type O blood has no antigens. The Rh blood group has either the Rh antigen (Rh+) or no Rh antigen (Rh–).

Exercise:

Problem: List some of the functions of blood in the body.

Solution:

Blood is important for regulation of the body's pH, temperature, and osmotic pressure, the circulation of nutrients and removal of wastes, the distribution of hormones from endocrine glands, the elimination of excess heat; it also contains components for the clotting of blood to prevent blood loss. Blood also transports clotting factors and disease-fighting agents.

Exercise:

Problem: How does the lymphatic system work with blood flow?

Solution:

Lymph capillaries take fluid from the blood to the lymph nodes. The lymph nodes filter the lymph by percolation through connective tissue filled with white blood cells. The white blood cells remove infectious agents, such as bacteria and viruses, to clean the lymph before it returns to the bloodstream.

Glossary

plasma
:   liquid component of blood that is left after the cells are removed

platelet
:   (also, thrombocyte) small cellular fragment that collects at wounds, cross-reacts with clotting factors, and forms a plug to prevent blood loss

red blood cell
:   small (7–8 μm) biconcave cell without mitochondria (and in mammals without nuclei) that is packed with hemoglobin, giving the cell its red color; transports oxygen through the body

serum
:   plasma without the coagulation factors

white blood cell
:   large (30 μm) cell with nuclei of which there are many types with different roles including the protection of the body from viruses and bacteria, and cleaning up dead cells and other waste

Mammalian Heart and Blood Vessels
By the end of this section, you will be able to:

- Describe the structure of the heart and explain how cardiac muscle is different from other muscles
- Describe the cardiac cycle
- Explain the structure of arteries, veins, and capillaries, and how blood flows through the body

The heart is a complex muscle that pumps blood through the three divisions of the circulatory system: the coronary (vessels that serve the heart), pulmonary (heart and lungs), and systemic (systems of the body), as shown in [link]. Coronary circulation intrinsic to the heart takes blood directly from the main artery (aorta) coming from the heart. For pulmonary and systemic circulation, the heart has to pump blood to the lungs or the rest of the body, respectively. In vertebrates, the lungs are relatively close to the heart in the thoracic cavity. The shorter distance to pump means that the muscle wall on the right side of the heart is not as thick as the left side which must have enough pressure to pump blood all the way to your big toe.

Note:
Art Connection
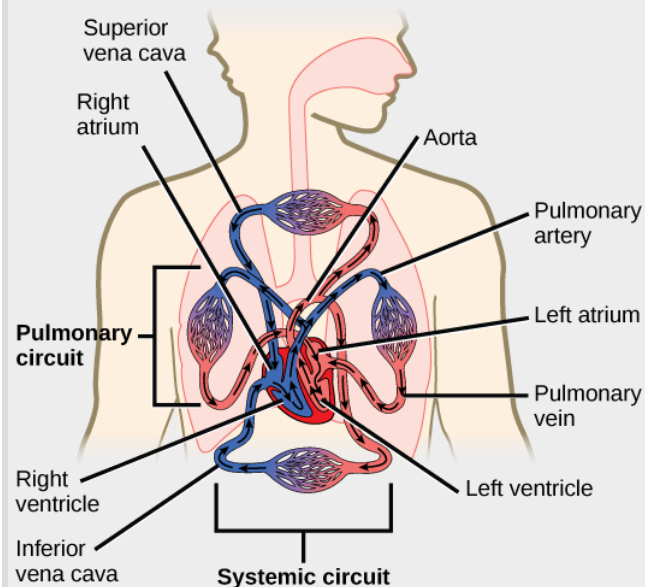
The mammalian circulatory system is divided into three circuits: the systemic circuit, the pulmonary circuit, and the coronary circuit. Blood is pumped from veins of the systemic circuit into the right atrium of the heart, then into the right ventricle. Blood then enters the pulmonary circuit, and is oxygenated by the lungs. From the pulmonary circuit, blood re-enters the heart through the left atrium. From the left ventricle, blood re-enters the systemic circuit through the aorta and is distributed to the rest of the body. The coronary circuit, which provides blood to the heart, is not shown.

Which of the following statements about the circulatory system is false?

a. Blood in the pulmonary vein is deoxygenated.
b. Blood in the inferior vena cava is deoxygenated.
c. Blood in the pulmonary artery is deoxygenated.
d. Blood in the aorta is oxygenated.

Structure of the Heart

The heart muscle is asymmetrical as a result of the distance blood must travel in the pulmonary and systemic circuits. Since the right side of the heart sends blood to the pulmonary circuit it is smaller than the left side which must send blood out to the whole body in the systemic circuit, as

shown in [link]. In humans, the heart is about the size of a clenched fist; it is divided into four chambers: two atria and two ventricles. There is one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The atria are the chambers that receive blood, and the ventricles are the chambers that pump blood. The right atrium receives deoxygenated blood from the **superior vena cava**, which drains blood from the jugular vein that comes from the brain and from the veins that come from the arms, as well as from the **inferior vena cava** which drains blood from the veins that come from the lower organs and the legs. In addition, the right atrium receives blood from the coronary sinus which drains deoxygenated blood from the heart itself. This deoxygenated blood then passes to the right ventricle through the **atrioventricular valve** or the **tricuspid valve**, a flap of connective tissue that opens in only one direction to prevent the backflow of blood. The valve separating the chambers on the left side of the heart valve is called the biscuspid or mitral valve. After it is filled, the right ventricle pumps the blood through the pulmonary arteries, by-passing the **semilunar valve** (or pulmonic valve) to the lungs for re-oxygenation. After blood passes through the pulmonary arteries, the right semilunar valves close preventing the blood from flowing backwards into the right ventricle. The left atrium then receives the oxygen-rich blood from the lungs via the pulmonary veins. This blood passes through the **bicuspid valve** or mitral valve (the atrioventricular valve on the left side of the heart) to the left ventricle where the blood is pumped out through **aorta**, the major artery of the body, taking oxygenated blood to the organs and muscles of the body. Once blood is pumped out of the left ventricle and into the aorta, the aortic semilunar valve (or aortic valve) closes preventing blood from flowing backward into the left ventricle. This pattern of pumping is referred to as double circulation and is found in all mammals.

> **Note:**
> Art Connection

Pulmonary artery

Superior vena cava

Right atrium

Pulmonary valve
(semilunar)

Tricuspid valve
(atrioventricular)

Right ventricle

Inferior vena cava

Aorta

Pulmonary artery

Left atrium

Aortic valve
(semilunar)

Mitral valve
(atrioventricular)

Left ventricle

Pericardium

Endocardium

Fibrous
pericardium

Pericardial
space

Parietal
pericardium

Myocardium

Epicardium

(a)

Coronary arteries

Cardiac veins

(b)

(a) The heart is primarily made of a thick muscle layer,
called the myocardium, surrounded by membranes. One-
way valves separate the four chambers. (b) Blood vessels of
the coronary system, including the coronary arteries and
veins, keep the heart musculature oxygenated.

Which of the following statements about the heart is false?

a. The mitral valve separates the left ventricle from the left atrium.
b. Blood travels through the bicuspid valve to the left atrium.
c. Both the aortic and the pulmonary valves are semilunar valves.
d. The mitral valve is an atrioventricular valve.

The heart is composed of three layers; the epicardium, the myocardium, and the endocardium, illustrated in [link]. The inner wall of the heart has a lining called the **endocardium**. The **myocardium** consists of the heart muscle cells that make up the middle layer and the bulk of the heart wall. The outer layer of cells is called the **epicardium**, of which the second layer is a membranous layered structure called the **pericardium** that surrounds and protects the heart; it allows enough room for vigorous pumping but also keeps the heart in place to reduce friction between the heart and other structures.

The heart has its own blood vessels that supply the heart muscle with blood. The **coronary arteries** branch from the aorta and surround the outer surface of the heart like a crown. They diverge into capillaries where the heart muscle is supplied with oxygen before converging again into the **coronary veins** to take the deoxygenated blood back to the right atrium where the blood will be re-oxygenated through the pulmonary circuit. The heart muscle will die without a steady supply of blood. **Atherosclerosis** is the blockage of an artery by the buildup of fatty plaques. Because of the size (narrow) of the coronary arteries and their function in serving the heart itself, atherosclerosis can be deadly in these arteries. The slowdown of blood flow and subsequent oxygen deprivation that results from atherosclerosis causes severe pain, known as **angina**, and complete blockage of the arteries will cause **myocardial infarction**: the death of cardiac muscle tissue, commonly known as a heart attack.

The Cardiac Cycle

The main purpose of the heart is to pump blood through the body; it does so in a repeating sequence called the cardiac cycle. The **cardiac cycle** is the

coordination of the filling and emptying of the heart of blood by electrical signals that cause the heart muscles to contract and relax. The human heart beats over 100,000 times per day. In each cardiac cycle, the heart contracts (**systole**), pushing out the blood and pumping it through the body; this is followed by a relaxation phase (**diastole**), where the heart fills with blood, as illustrated in [link]. The atria contract at the same time, forcing blood through the atrioventricular valves into the ventricles. Closing of the atrioventricular valves produces a monosyllabic "lup" sound. Following a brief delay, the ventricles contract at the same time forcing blood through the semilunar valves into the aorta and the artery transporting blood to the lungs (via the pulmonary artery). Closing of the semilunar valves produces a monosyllabic "dup" sound.

(a) **Cardiac diastole**: all chambers are relaxed, and blood flows into the heart.

(b) **Atrial systole, ventricular diastole**: atria contract, pushing blood into the ventricles.

(c) **Atrial diastole, ventricular systole**: after the atria relax, the ventricles contract, pushing blood out of the heart.
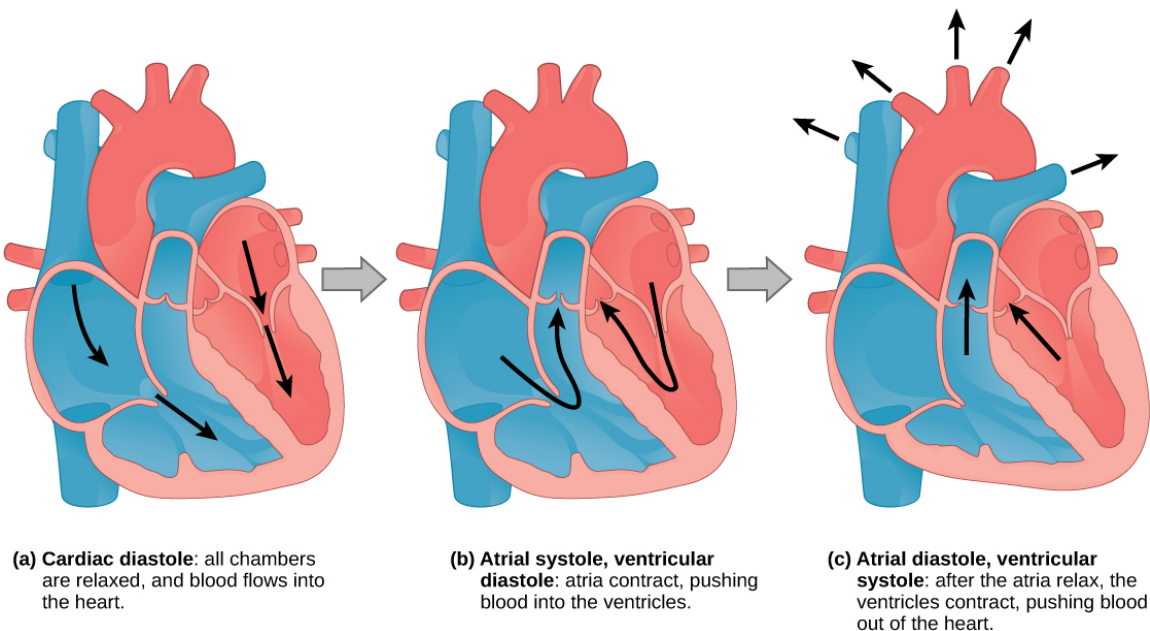
During (a) cardiac diastole, the heart muscle is relaxed and blood flows into the heart. During (b) atrial systole, the atria contract, pushing blood into the ventricles. During (c) atrial diastole, the ventricles contract, forcing blood out of the heart.

The pumping of the heart is a function of the cardiac muscle cells, or cardiomyocytes, that make up the heart muscle. **Cardiomyocytes**, shown in [link], are distinctive muscle cells that are striated like skeletal muscle but pump rhythmically and involuntarily like smooth muscle; they are connected by intercalated disks exclusive to cardiac muscle. They are self-stimulated for a period of time and isolated cardiomyocytes will beat if given the correct balance of nutrients and electrolytes.
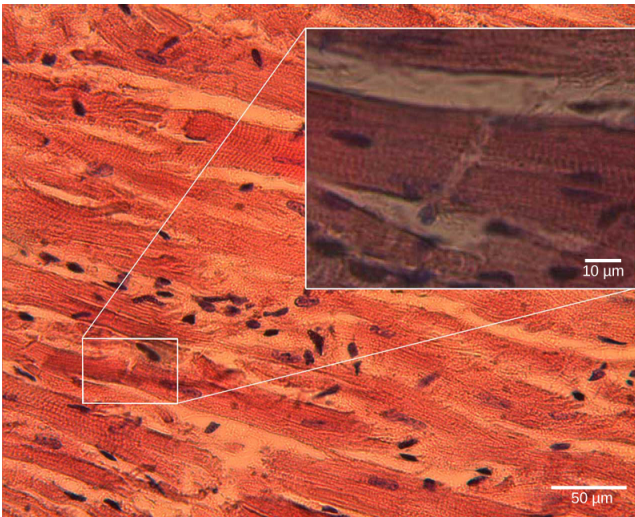
Cardiomyocytes are striated muscle cells found in cardiac tissue. (credit: modification of work by Dr. S. Girod, Anton Becker; scale-bar data from Matt Russell)

The autonomous beating of cardiac muscle cells is regulated by the heart's internal pacemaker that uses electrical signals to time the beating of the heart. The electrical signals and mechanical actions, illustrated in [link], are intimately intertwined. The internal pacemaker starts at the **sinoatrial (SA) node**, which is located near the wall of the right atrium. Electrical charges spontaneously pulse from the SA node causing the two atria to contract in

unison. The pulse reaches a second node, called the atrioventricular (AV) node, between the right atrium and right ventricle where it pauses for approximately 0.1 second before spreading to the walls of the ventricles. From the AV node, the electrical impulse enters the bundle of His, then to the left and right bundle branches extending through the interventricular septum. Finally, the Purkinje fibers conduct the impulse from the apex of the heart up the ventricular myocardium, and then the ventricles contract. This pause allows the atria to empty completely into the ventricles before the ventricles pump out the blood. The electrical impulses in the heart produce electrical currents that flow through the body and can be measured on the skin using electrodes. This information can be observed as an **electrocardiogram (ECG)**—a recording of the electrical impulses of the cardiac muscle.

(a) An electrical impulse travels from the sinoatrial node to the walls of the atria, causing them to contract.

(b) The impulse reaches the atrioventricular node, which delays it by about 0.1 second.

(c) Bundle branches carry signals from the atrioventricular node to the heart apex.

(d) The signal spreads through the ventricle walls, causing them to contract.
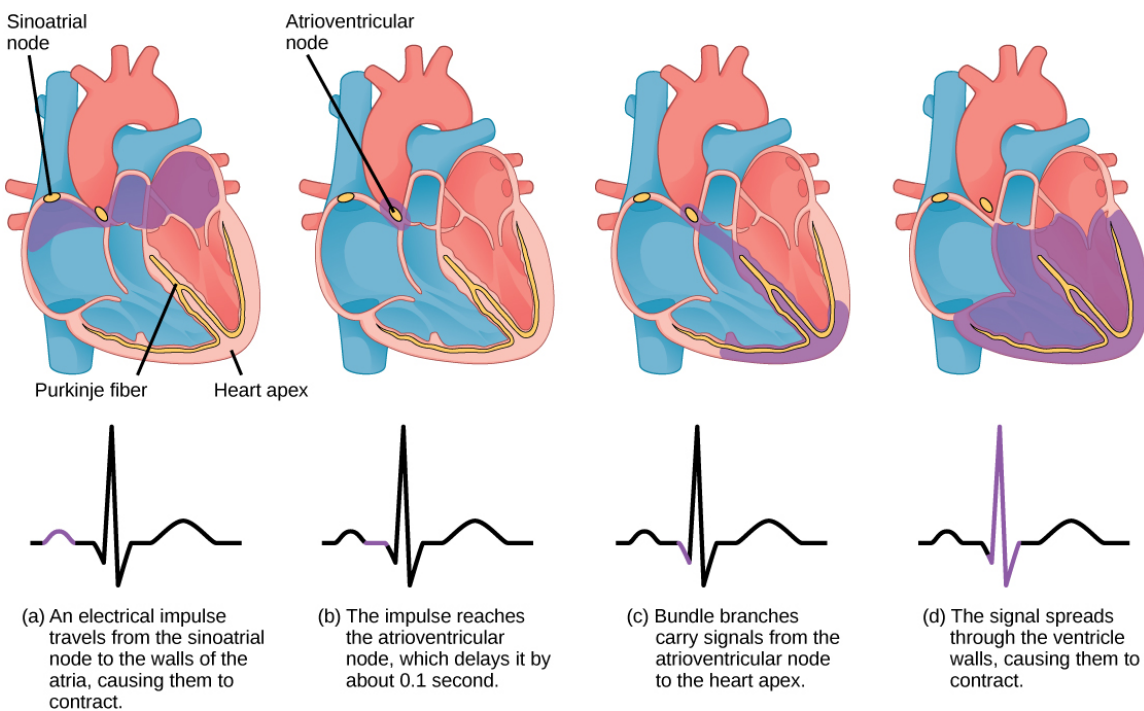
The beating of the heart is regulated by an electrical impulse that causes the characteristic reading of an ECG. The signal is initiated at the sinoatrial valve. The signal then (a) spreads to the atria, causing them to contract. The signal is (b) delayed at the atrioventricular node before it is passed on to the (c) heart apex.

The delay allows the atria to relax before the (d) ventricles contract. The final part of the ECG cycle prepares the heart for the next beat.

Arteries, Veins, and Capillaries

The blood from the heart is carried through the body by a complex network of blood vessels ([link]). **Arteries** take blood away from the heart. The main artery is the aorta that branches into major arteries that take blood to different limbs and organs. These major arteries include the carotid artery that takes blood to the brain, the brachial arteries that take blood to the arms, and the thoracic artery that takes blood to the thorax and then into the hepatic, renal, and gastric arteries for the liver, kidney, and stomach, respectively. The iliac artery takes blood to the lower limbs. The major arteries diverge into minor arteries, and then smaller vessels called **arterioles**, to reach more deeply into the muscles and organs of the body.
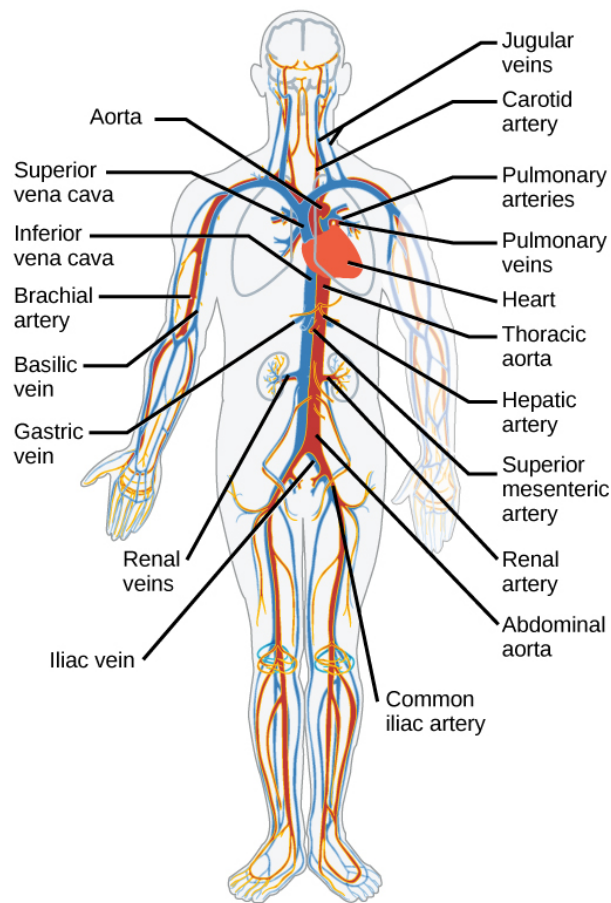
The major human arteries and veins are shown. (credit: modification of work by Mariana Ruiz Villareal)

Arterioles diverge into capillary beds. **Capillary beds** contain a large number (10 to 100) of **capillaries** that branch among the cells and tissues of the body. Capillaries are narrow-diameter tubes that can fit red blood cells through in single file and are the sites for the exchange of nutrients, waste, and oxygen with tissues at the cellular level. Fluid also crosses into the interstitial space from the capillaries. The capillaries converge again into **venules** that connect to minor veins that finally connect to major veins that take blood high in carbon dioxide back to the heart. **Veins** are blood vessels that bring blood back to the heart. The major veins drain blood from the

same organs and limbs that the major arteries supply. Fluid is also brought back to the heart via the lymphatic system.

The structure of the different types of blood vessels reflects their function or layers. There are three distinct layers, or tunics, that form the walls of blood vessels ([link]). The first tunic is a smooth, inner lining of endothelial cells that are in contact with the red blood cells. The endothelial tunic is continuous with the endocardium of the heart. In capillaries, this single layer of cells is the location of diffusion of oxygen and carbon dioxide between the endothelial cells and red blood cells, as well as the exchange site via endocytosis and exocytosis. The movement of materials at the site of capillaries is regulated by **vasoconstriction**, narrowing of the blood vessels, and **vasodilation**, widening of the blood vessels; this is important in the overall regulation of blood pressure.

Veins and arteries both have two further tunics that surround the endothelium: the middle tunic is composed of smooth muscle and the outermost layer is connective tissue (collagen and elastic fibers). The elastic connective tissue stretches and supports the blood vessels, and the smooth muscle layer helps regulate blood flow by altering vascular resistance through vasoconstriction and vasodilation. The arteries have thicker smooth muscle and connective tissue than the veins to accommodate the higher pressure and speed of freshly pumped blood. The veins are thinner walled as the pressure and rate of flow are much lower. In addition, veins are structurally different than arteries in that veins have valves to prevent the backflow of blood. Because veins have to work against gravity to get blood back to the heart, contraction of skeletal muscle assists with the flow of blood back to the heart.
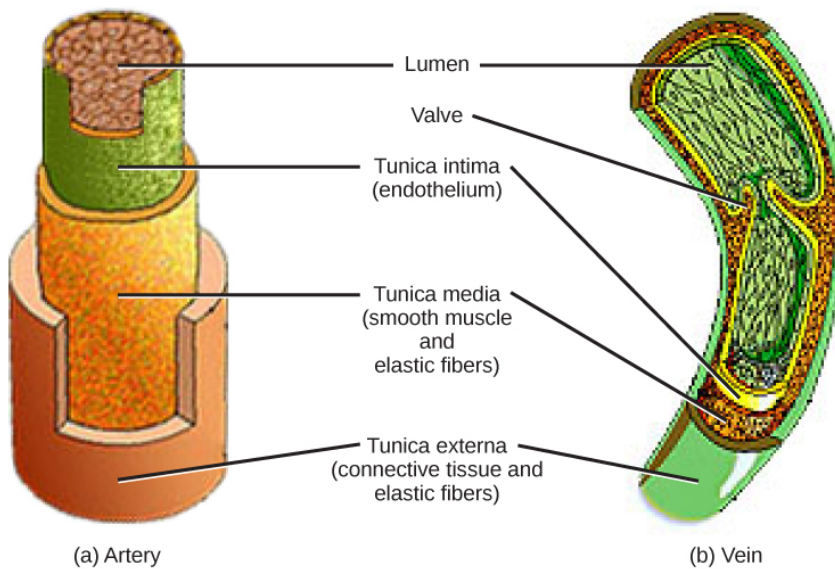
Arteries and veins consist of three layers: an outer tunica externa, a middle tunica media, and an inner tunica intima. Capillaries consist of a single layer of epithelial cells, the tunica intima. (credit: modification of work by NCI, NIH)

Section Summary

The heart muscle pumps blood through three divisions of the circulatory system: coronary, pulmonary, and systemic. There is one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The pumping of the heart is a function of cardiomyocytes, distinctive muscle cells that are striated like skeletal muscle but pump rhythmically and involuntarily like smooth muscle. The internal pacemaker starts at the sinoatrial node, which is located near the wall of the right atrium. Electrical charges pulse from the SA node causing the two atria to contract in unison; then the pulse reaches the atrioventricular node between the right atrium and right ventricle. A pause in the electric signal allows the atria to empty completely into the ventricles before the ventricles pump out the blood. The blood from the heart is carried through the body by a complex network of

blood vessels; arteries take blood away from the heart, and veins bring blood back to the heart.

Art Connections

Exercise:

  Problem:

  [link] Which of the following statements about the circulatory system is false?

   a. Blood in the pulmonary vein is deoxygenated.
   b. Blood in the inferior vena cava is deoxygenated.
   c. Blood in the pulmonary artery is deoxygenated.
   d. Blood in the aorta is oxygenated.

  Solution:

  [link] C

Exercise:

  Problem:

  [link] Which of the following statements about the heart is false?

   a. The mitral valve separates the left ventricle from the left atrium.
   b. Blood travels through the bicuspid valve to the left atrium.
   c. Both the aortic and the pulmonary valves are semilunar valves.
   d. The mitral valve is an atrioventricular valve.

  Solution:

  [link] B

Review Questions

Exercise:

Problem: The heart's internal pacemaker beats by:

   a. an internal implant that sends an electrical impulse through the
      heart
   b. the excitation of cardiac muscle cells at the sinoatrial node
      followed by the atrioventricular node
   c. the excitation of cardiac muscle cells at the atrioventricular node
      followed by the sinoatrial node
   d. the action of the sinus

Solution:

   B

Exercise:

   Problem:

During the systolic phase of the cardiac cycle, the heart is _____.

   a. contracting
   b. relaxing
   c. contracting and relaxing
   d. filling with blood

Solution:

   A

Exercise:

Problem: Cardiomyocytes are similar to skeletal muscle because:

   a. they beat involuntarily
   b. they are used for weight lifting

c. they pulse rhythmically
d. they are striated

Solution:

D

Exercise:

Problem: How do arteries differ from veins?

a. Arteries have thicker smooth muscle layers to accommodate the changes in pressure from the heart.
b. Arteries carry blood.
c. Arteries have thinner smooth muscle layers and valves and move blood by the action of skeletal muscle.
d. Arteries are thin walled and are used for gas exchange.

Solution:

A

Free Response

Exercise:

Problem: Describe the cardiac cycle.

Solution:

The heart receives an electrical signal from the sinoatrial node triggering the cardiac muscle cells in the atria to contract. The signal pauses at the atrioventricular node before spreading to the walls of the ventricles so the blood is pumped through the body. This is the systolic phase. The heart then relaxes in the diastole and fills again with blood.

Exercise:

Problem: What happens in capillaries?

Solution:

The capillaries basically exchange materials with their surroundings. Their walls are very thin and are made of one or two layers of cells, where gases, nutrients, and waste are diffused. They are distributed as beds, complex networks that link arteries as well as veins.

Glossary

angina
      pain caused by partial blockage of the coronary arteries by the buildup
      of plaque and lack of oxygen to the heart muscle

aorta
      major artery of the body that takes blood away from the heart

arteriole
      small vessel that connects an artery to a capillary bed

artery
      blood vessel that takes blood away from the heart

atherosclerosis
      buildup of fatty plaques in the coronary arteries in the heart

atrioventricular valve
      one-way membranous flap of connective tissue between the atrium and
      the ventricle in the right side of the heart; also known as tricuspid
      valve

bicuspid valve
      (also, mitral valve; left atrioventricular valve) one-way membranous
      flap between the atrium and the ventricle in the left side of the heart

capillary

    smallest blood vessel that allows the passage of individual blood cells
and the site of diffusion of oxygen and nutrient exchange

capillary bed

    large number of capillaries that converge to take blood to a particular
organ or tissue

cardiac cycle

    filling and emptying the heart of blood by electrical signals that cause
the heart muscles to contract and relax

cardiomyocyte

    specialized heart muscle cell that is striated but contracts involuntarily
like smooth muscle

coronary artery

    vessel that supplies the heart tissue with blood

coronary vein

    vessel that takes blood away from the heart tissue back to the
chambers in the heart

diastole

    relaxation phase of the cardiac cycle when the heart is relaxed and the
ventricles are filling with blood

electrocardiogram (ECG)

    recording of the electrical impulses of the cardiac muscle

endocardium

    innermost layer of tissue in the heart

epicardium

    outermost tissue layer of the heart

inferior vena cava

drains blood from the veins that come from the lower organs and the legs

myocardial infarction
    (also, heart attack) complete blockage of the coronary arteries and death of the cardiac muscle tissue

myocardium
    heart muscle cells that make up the middle layer and the bulk of the heart wall

pericardium
    membrane layer protecting the heart; also part of the epicardium

semilunar valve
    membranous flap of connective tissue between the aorta and a ventricle of the heart (the aortic or pulmonary semilunar valves)

sinoatrial (SA) node
    the heart's internal pacemaker; located near the wall of the right atrium

superior vena cava
    drains blood from the jugular vein that comes from the brain and from the veins that come from the arms

systole
    contraction phase of cardiac cycle when the ventricles are pumping blood into the arteries

tricuspid valve
    one-way membranous flap of connective tissue between the atrium and the ventricle in the right side of the heart; also known as atrioventricular valve

vasoconstriction
    narrowing of a blood vessel

vasodilation

widening of a blood vessel

vein

blood vessel that brings blood back to the heart

vena cava

major vein of the body returning blood from the upper and lower parts
of the body; see the superior vena cava and inferior vena cava

venule

blood vessel that connects a capillary bed to a vein

Blood Flow and Blood Pressure Regulation
By the end of this section, you will be able to:

- Describe the system of blood flow through the body
- Describe how blood pressure is regulated

Blood pressure (BP) is the pressure exerted by blood on the walls of a blood vessel that helps to push blood through the body. Systolic blood pressure measures the amount of pressure that blood exerts on vessels while the heart is beating. The optimal systolic blood pressure is 120 mmHg. Diastolic blood pressure measures the pressure in the vessels between heartbeats. The optimal diastolic blood pressure is 80 mmHg. Many factors can affect blood pressure, such as hormones, stress, exercise, eating, sitting, and standing. Blood flow through the body is regulated by the size of blood vessels, by the action of smooth muscle, by one-way valves, and by the fluid pressure of the blood itself.

How Blood Flows Through the Body

Blood is pushed through the body by the action of the pumping heart. With each rhythmic pump, blood is pushed under high pressure and velocity away from the heart, initially along the main artery, the aorta. In the aorta, the blood travels at 30 cm/sec. As blood moves into the arteries, arterioles, and ultimately to the capillary beds, the rate of movement slows dramatically to about 0.026 cm/sec, one-thousand times slower than the rate of movement in the aorta. While the diameter of each individual arteriole and capillary is far narrower than the diameter of the aorta, and according to the law of continuity, fluid should travel faster through a narrower diameter tube, the rate is actually slower due to the overall diameter of all the combined capillaries being far greater than the diameter of the individual aorta.

The slow rate of travel through the capillary beds, which reach almost every cell in the body, assists with gas and nutrient exchange and also promotes the diffusion of fluid into the interstitial space. After the blood has passed through the capillary beds to the venules, veins, and finally to the main venae cavae, the rate of flow increases again but is still much slower than

the initial rate in the aorta. Blood primarily moves in the veins by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Because most veins must move blood against the pull of gravity, blood is prevented from flowing backward in the veins by one-way valves. Because skeletal muscle contraction aids in venous blood flow, it is important to get up and move frequently after long periods of sitting so that blood will not pool in the extremities.

Blood flow through the capillary beds is regulated depending on the body's needs and is directed by nerve and hormone signals. For example, after a large meal, most of the blood is diverted to the stomach by vasodilation of vessels of the digestive system and vasoconstriction of other vessels. During exercise, blood is diverted to the skeletal muscles through vasodilation while blood to the digestive system would be lessened through vasoconstriction. The blood entering some capillary beds is controlled by small muscles, called precapillary sphincters, illustrated in [link]. If the sphincters are open, the blood will flow into the associated branches of the capillary blood. If all of the sphincters are closed, then the blood will flow directly from the arteriole to the venule through the thoroughfare channel (see [link]). These muscles allow the body to precisely control when capillary beds receive blood flow. At any given moment only about 5-10% of our capillary beds actually have blood flowing through them.

Note:
Art Connection
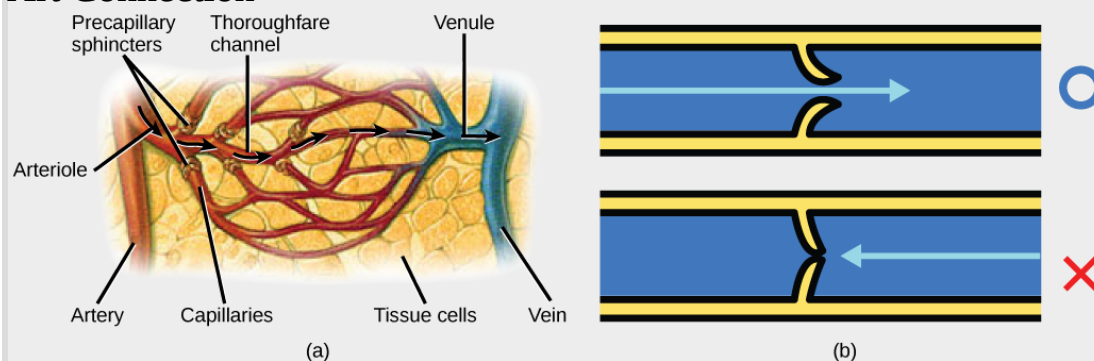
(a) Precapillary sphincters are rings of smooth muscle that regulate the flow of blood through capillaries; they help control

the location of blood flow to where it is needed. (b) Valves in the veins prevent blood from moving backward. (credit a: modification of work by NCI)

Varicose veins are veins that become enlarged because the valves no longer close properly, allowing blood to flow backward. Varicose veins are often most prominent on the legs. Why do you think this is the case?

Proteins and other large solutes cannot leave the capillaries. The loss of the watery plasma creates a hyperosmotic solution within the capillaries, especially near the venules. This causes about 85% of the plasma that leaves the capillaries to eventually diffuses back into the capillaries near the venules. The remaining 15% of blood plasma drains out from the interstitial fluid into nearby lymphatic vessels ([link]). The fluid in the lymph is similar in composition to the interstitial fluid. The lymph fluid passes through lymph nodes before it returns to the heart via the vena cava. **Lymph nodes** are specialized organs that filter the lymph by percolation through a maze of connective tissue filled with white blood cells. The white blood cells remove infectious agents, such as bacteria and viruses, to clean the lymph before it returns to the bloodstream. After it is cleaned, the lymph

returns to the heart by the action of smooth muscle pumping, skeletal muscle action, and one-way valves joining the returning blood near the junction of the venae cavae entering the right atrium of the heart.
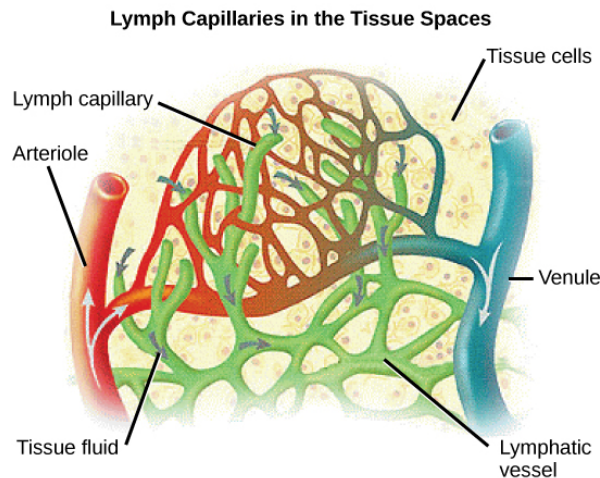
Fluid from the capillaries moves into the interstitial space and lymph capillaries by diffusion down a pressure gradient and also by osmosis. Out of 7,200 liters of fluid pumped by the average heart in a day, over 1,500 liters is filtered. (credit: modification of work by NCI, NIH)

Note:
Evolution Connection
Vertebrate Diversity in Blood Circulation
Blood circulation has evolved differently in vertebrates and may show variation in different animals for the required amount of pressure, organ

and vessel location, and organ size. Animals with longs necks and those that live in cold environments have distinct blood pressure adaptations. Long necked animals, such as giraffes, need to pump blood upward from the heart against gravity. The blood pressure required from the pumping of the left ventricle would be equivalent to 250 mm Hg (mm Hg = millimeters of mercury, a unit of pressure) to reach the height of a giraffe's head, which is 2.5 meters higher than the heart. However, if checks and balances were not in place, this blood pressure would damage the giraffe's brain, particularly if it was bending down to drink. These checks and balances include valves and feedback mechanisms that reduce the rate of cardiac output. Long-necked dinosaurs such as the sauropods had to pump blood even higher, up to ten meters above the heart. This would have required a blood pressure of more than 600 mm Hg, which could only have been achieved by an enormous heart. Evidence for such an enormous heart does not exist and mechanisms to reduce the blood pressure required include the slowing of metabolism as these animals grew larger. It is likely that they did not routinely feed on tree tops but grazed on the ground.

Living in cold water, whales need to maintain the temperature in their blood. This is achieved by the veins and arteries being close together so that heat exchange can occur. This mechanism is called a countercurrent heat exchanger. The blood vessels and the whole body are also protected by thick layers of blubber to prevent heat loss. In land animals that live in cold environments, thick fur and hibernation are used to retain heat and slow metabolism.

Blood Pressure

The pressure of the blood flow in the body is produced by the hydrostatic pressure of the fluid (blood) against the walls of the blood vessels. Fluid will move from areas of high to low hydrostatic pressures. In the arteries, the hydrostatic pressure near the heart is very high and blood flows to the arterioles where the rate of flow is slowed by the narrow openings of the arterioles. During systole, when new blood is entering the arteries, the artery walls stretch to accommodate the increase of pressure of the extra blood; during diastole, the walls return to normal because of their elastic

properties. The blood pressure of the systole phase and the diastole phase, graphed in [link], gives the two pressure readings for blood pressure. For example, 120/80 indicates a reading of 120 mm Hg during the systole and 80 mm Hg during diastole. Throughout the cardiac cycle, the blood continues to empty into the arterioles at a relatively even rate. This resistance to blood flow is called **peripheral resistance**.
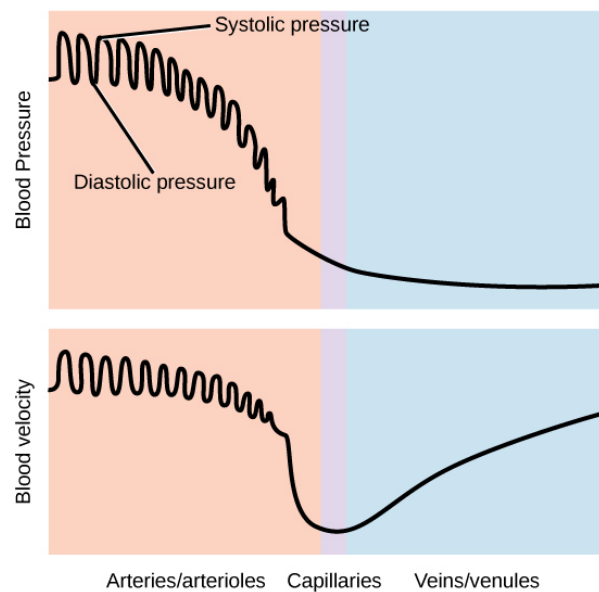
Blood pressure is related to the blood velocity in the arteries and arterioles. In the capillaries and veins, the blood pressure continues to decease but velocity increases.

Blood Pressure Regulation

Cardiac output is the volume of blood pumped by the heart in one minute. It is calculated by multiplying the number of heart contractions that occur per minute (heart rate) times the **stroke volume** (the volume of blood pumped

into the aorta per contraction of the left ventricle). Therefore, cardiac output can be increased by increasing heart rate, as when exercising. However, cardiac output can also be increased by increasing stroke volume, such as if the heart contracts with greater strength. Stroke volume can also be increased by speeding blood circulation through the body so that more blood enters the heart between contractions. During heavy exertion, the blood vessels relax and increase in diameter, offsetting the increased heart rate and ensuring adequate oxygenated blood gets to the muscles. Stress triggers a decrease in the diameter of the blood vessels, consequently increasing blood pressure. These changes can also be caused by nerve signals or hormones, and even standing up or lying down can have a great effect on blood pressure.

Section Summary

Blood primarily moves through the body by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Blood is prevented from flowing backward in the veins by one-way valves. Blood flow through the capillary beds is controlled by precapillary sphincters to increase and decrease flow depending on the body's needs and is directed by nerve and hormone signals. Lymph vessels take fluid that has leaked out of the blood to the lymph nodes where it is cleaned before returning to the heart. During systole, blood enters the arteries, and the artery walls stretch to accommodate the extra blood. During diastole, the artery walls return to normal. The blood pressure of the systole phase and the diastole phase gives the two pressure readings for blood pressure.

Art Connections

Exercise:

Problem:

[link] Varicose veins are veins that become enlarged because the valves no longer close properly, allowing blood to flow backward. Varicose veins are often most prominent on the legs. Why do you think this is the case?

Solution:

[link] Blood in the legs is farthest away from the heart and has to flow up to reach it.

Review Questions

Exercise:

Problem: High blood pressure would be a result of _____.

    a. a high cardiac output and high peripheral resistance
    b. a high cardiac output and low peripheral resistance
    c. a low cardiac output and high peripheral resistance
    d. a low cardiac output and low peripheral resistance

Solution:

A

Free Response

Exercise:

Problem: How does blood pressure change during heavy exercise?

Solution:

The heart rate increases, which increases the hydrostatic pressure against the artery walls. At the same time, the arterioles dilate in response to the increased exercise, which reduces peripheral resistance.

Glossary

blood pressure (BP)
>   pressure of blood in the arteries that helps to push blood through the body

cardiac output
>   the volume of blood pumped by the heart in one minute as a product of heart rate multiplied by stroke volume

lymph node
>   specialized organ that contains a large number of macrophages that clean the lymph before the fluid is returned to the heart

peripheral resistance
>   resistance of the artery and blood vessel walls to the pressure placed on them by the force of the heart pumping

precapillary sphincter
>   small muscle that controls blood circulation in the capillary beds

stroke volume>
>   - the volume of blood pumped into the aorta per contraction of the left ventricle

Introduction
class="introduction"

Lungs, which appear as nearly transparent tissue surrounding the heart in this X-ray of a dog (left), are the central organs of the respiratory system. The left lung is smaller than the right lung to accommodate space for the heart. A dog's nose (right) has a slit on the side of each nostril. When tracking a scent, the slits open, blocking the front of the nostrils. This allows the dog to exhale

though the now-open area on the side of the nostrils without losing the scent that is being followed. (credit a: modification of work by Geoff Stearns; credit b: modification of work by Cory Zanker)

Breathing is an involuntary event. How often a breath is taken and how much air is inhaled or exhaled are tightly regulated by the respiratory center in the brain. Humans, when they aren't exerting themselves, breathe

approximately 15 times per minute on average. Canines, like the dog in [link], have a respiratory rate of about 15–30 breaths per minute. With every inhalation, air fills the lungs, and with every exhalation, air rushes back out. That air is doing more than just inflating and deflating the lungs in the chest cavity. The air contains oxygen that crosses the lung tissue, enters the bloodstream, and travels to organs and tissues. Oxygen (O_2) enters the cells where it is used for metabolic reactions that produce ATP, a high-energy compound. At the same time, these reactions release carbon dioxide (CO_2) as a by-product. CO_2 is toxic and must be eliminated. Carbon dioxide exits the cells, enters the bloodstream, travels back to the lungs, and is expired out of the body during exhalation.

Systems of Gas Exchange
By the end of this section, you will be able to:

- Describe the passage of air from the outside environment to the lungs
- Explain how the lungs are protected from particulate matter

The primary function of the respiratory system is to deliver oxygen to the cells of the body's tissues and remove carbon dioxide, a cell waste product. The main structures of the human respiratory system are the nasal cavity, the trachea, and lungs.

All aerobic organisms require oxygen to carry out their metabolic functions. Along the evolutionary tree, different organisms have devised different means of obtaining oxygen from the surrounding atmosphere. The environment in which the animal lives greatly determines how an animal respires. The complexity of the respiratory system is correlated with the size of the organism. As animal size increases, diffusion distances increase and the ratio of surface area to volume drops. In unicellular organisms, diffusion across the cell membrane is sufficient for supplying oxygen to the cell ([link]). Diffusion is a slow, passive transport process. In order for diffusion to be a feasible means of providing oxygen to the cell, the rate of oxygen uptake must match the rate of diffusion across the membrane. In other words, if the cell were very large or thick, diffusion would not be able to provide oxygen quickly enough to the inside of the cell. Therefore, dependence on diffusion as a means of obtaining oxygen and removing carbon dioxide remains feasible only for small organisms or those with highly-flattened bodies, such as many flatworms (Platyhelminthes). Larger organisms had to evolve specialized respiratory tissues, such as gills, lungs, and respiratory passages accompanied by complex circulatory systems, to transport oxygen throughout their entire body.

The cell of the unicellular algae *Ventricaria ventricosa* is one of the largest known, reaching one to five centimeters in diameter. Like all single-celled organisms, *V. ventricosa* exchanges gases across the cell membrane.

Direct Diffusion

For small multicellular organisms, diffusion across the outer membrane is sufficient to meet their oxygen needs. Gas exchange by direct diffusion across surface membranes is efficient for organisms less than 1 mm in diameter. In simple organisms, such as cnidarians and flatworms, every cell in the body is close to the external environment. Their cells are kept moist and gases diffuse quickly via direct diffusion. Flatworms are small, literally flat worms, which 'breathe' through diffusion across the outer membrane ([link]). The flat shape of these organisms increases the surface area for diffusion, ensuring that each cell within the body is close to the outer membrane surface and has access to oxygen. If the flatworm had a

cylindrical body, then the cells in the center would not be able to get oxygen.

This flatworm's process of respiration works by diffusion across the outer membrane. (credit: Stephen Childs)

Skin and Gills

Earthworms and amphibians use their skin (integument) as a respiratory organ. A dense network of capillaries lies just below the skin and facilitates gas exchange between the external environment and the circulatory system. The respiratory surface must be kept moist in order for the gases to dissolve and diffuse across cell membranes.

Organisms that live in water need to obtain oxygen from the water. Oxygen dissolves in water but at a lower concentration than in the atmosphere. The atmosphere has roughly 21 percent oxygen. In water, the oxygen concentration is much smaller than that. Fish and many other aquatic organisms have evolved gills to take up the dissolved oxygen from water ([link]). Gills are thin tissue filaments that are highly branched and folded. When water passes over the gills, the dissolved oxygen in water rapidly

diffuses across the gills into the bloodstream. The circulatory system can then carry the oxygenated blood to the other parts of the body. In animals that contain coelomic fluid instead of blood, oxygen diffuses across the gill surfaces into the coelomic fluid. Gills are found in mollusks, annelids, and crustaceans.

This common carp, like many other aquatic organisms, has gills that allow it to obtain oxygen from water. (credit: "Guitardude012"/Wikimedia Commons)

The folded surfaces of the gills provide a large surface area to ensure that the fish gets sufficient oxygen. Diffusion is a process in which material travels from regions of high concentration to low concentration until equilibrium is reached. In this case, blood with a low concentration of oxygen molecules circulates through the gills. The concentration of oxygen molecules in water is higher than the concentration of oxygen molecules in gills. As a result, oxygen molecules diffuse from water (high concentration) to blood (low concentration), as shown in [link]. Similarly, carbon dioxide

molecules in the blood diffuse from the blood (high concentration) to water (low concentration).
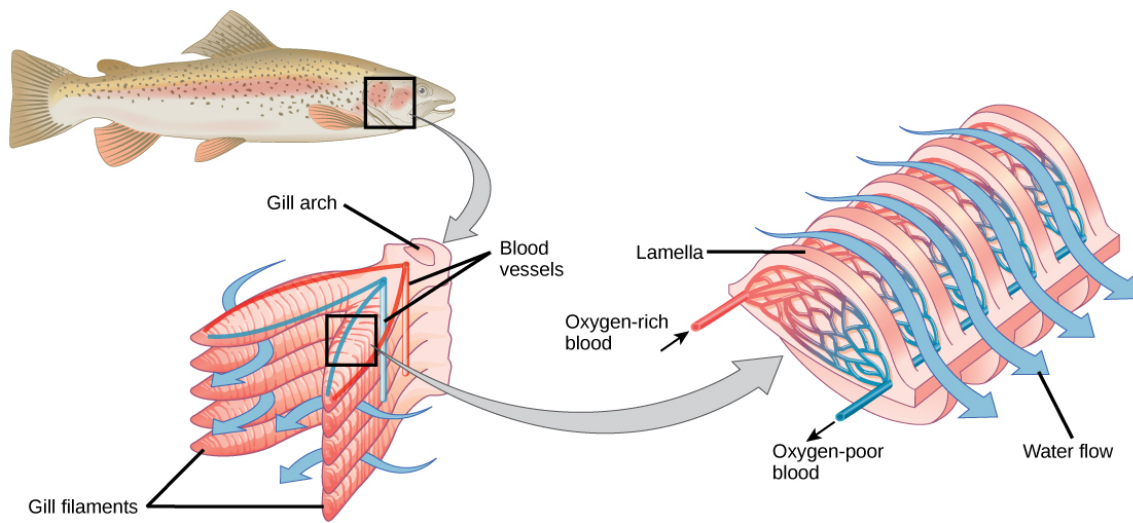
As water flows over the gills, oxygen is transferred to blood via the veins. (credit "fish": modification of work by Duane Raver, NOAA)

Tracheal Systems

Insect respiration is independent of its circulatory system; therefore, the blood does not play a direct role in oxygen transport. Insects have a highly specialized type of respiratory system called the tracheal system, which consists of a network of small tubes that carries oxygen to the entire body. The tracheal system is the most direct and efficient respiratory system in active animals. The tubes in the tracheal system are made of a polymeric material called chitin.

Insect bodies have openings, called spiracles, along the thorax and abdomen. These openings connect to the tubular network, allowing oxygen to pass into the body ([link]) and regulating the diffusion of CO_2 and water

vapor. Air enters and leaves the tracheal system through the spiracles. Some insects can ventilate the tracheal system with body movements.
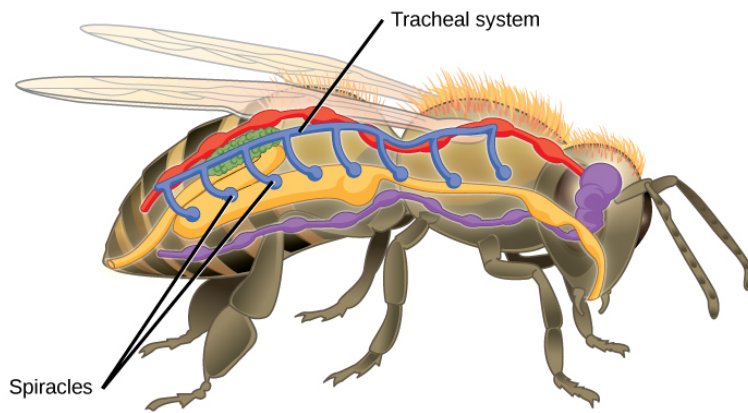
Insects perform respiration via a tracheal system.

Mammalian Systems

In mammals, pulmonary ventilation occurs via inhalation (breathing). During inhalation, air enters the body through the **nasal cavity** located just inside the nose ([link]). As air passes through the nasal cavity, the air is warmed to body temperature and humidified. The respiratory tract is coated with mucus to seal the tissues from direct contact with air. Mucus is high in water. As air crosses these surfaces of the mucous membranes, it picks up water. These processes help equilibrate the air to the body conditions, reducing any damage that cold, dry air can cause. Particulate matter that is floating in the air is removed in the nasal passages via mucus and cilia. The processes of warming, humidifying, and removing particles are important protective mechanisms that prevent damage to the trachea and lungs. Thus, inhalation serves several purposes in addition to bringing oxygen into the respiratory system.

Note:
Art Connection
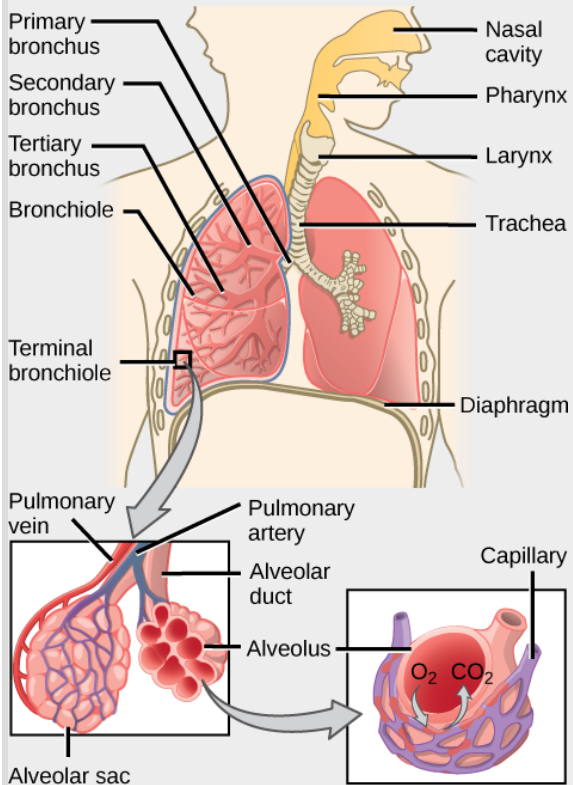
Air enters the respiratory system through the nasal cavity and pharynx, and then passes through the trachea and into the bronchi, which bring air into the lungs. (credit: modification of work by NCI)

Which of the following statements about the mammalian respiratory system is false?

a. When we breathe in, air travels from the pharynx to the trachea.
b. The bronchioles branch into bronchi.
c. Alveolar ducts connect to alveolar sacs.
d. Gas exchange between the lung and blood takes place in the alveolus.

From the nasal cavity, air passes through the **pharynx** (throat) and the **larynx** (voice box), as it makes its way to the **trachea** ([link]). The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder about 10 to 12 cm long and 2 cm in diameter that sits in front of the esophagus and extends from the larynx into the chest cavity where it divides into the two primary bronchi at the midthorax. It is made of incomplete rings of hyaline cartilage and smooth muscle ([link]). The trachea is lined with mucus-producing goblet cells and ciliated epithelia. The cilia propel foreign particles trapped in the mucus toward the pharynx. The cartilage provides strength and support to the trachea to keep the passage open. The smooth muscle can contract, decreasing the trachea's diameter, which causes expired air to rush upwards from the lungs at a great force. The forced exhalation helps expel mucus when we cough. Smooth muscle can contract or relax, depending on stimuli from the external environment or the body's nervous system.
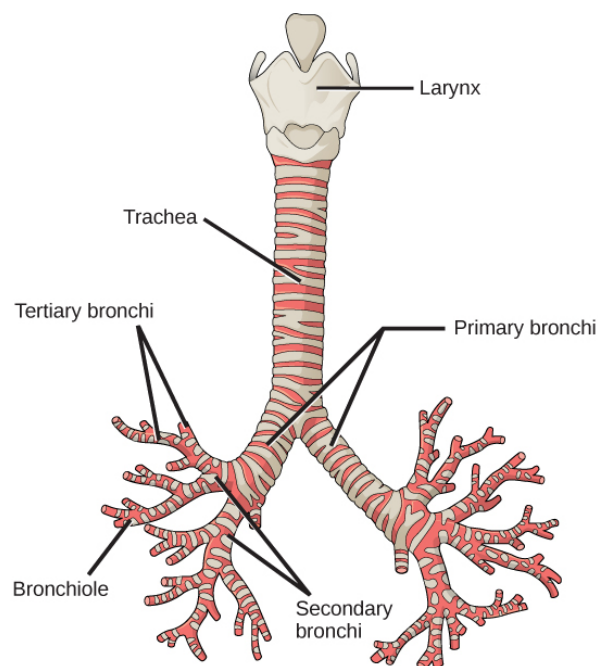
The trachea and bronchi are made of incomplete rings of cartilage. (credit: modification of work by Gray's Anatomy)

Lungs: Bronchi and Alveoli

The end of the trachea bifurcates (divides) to the right and left lungs. The lungs are not identical. The right lung is larger and contains three lobes, whereas the smaller left lung contains two lobes ([link]). The muscular **diaphragm**, which facilitates breathing, is inferior to (below) the lungs and marks the end of the thoracic cavity.
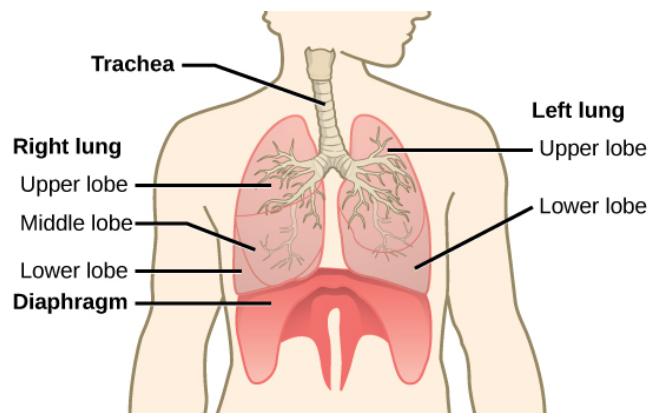
The trachea bifurcates into the right and left bronchi in the lungs. The right lung is made of three lobes and is larger. To accommodate the heart, the left lung is smaller and has only two lobes.

In the lungs, air is diverted into smaller and smaller passages, or **bronchi**. Air enters the lungs through the two **primary (main) bronchi** (singular: bronchus). Each bronchus divides into secondary bronchi, then into tertiary bronchi, which in turn divide, creating smaller and smaller diameter **bronchioles** as they split and spread through the lung. Like the trachea, the bronchi are made of cartilage and smooth muscle. At the bronchioles, the cartilage is replaced with elastic fibers. Bronchi are innervated by nerves of both the parasympathetic and sympathetic nervous systems that control muscle contraction (parasympathetic) or relaxation (sympathetic) in the bronchi and bronchioles, depending on the nervous system's cues. In humans, bronchioles with a diameter smaller than 0.5 mm are the **respiratory bronchioles**. They lack cartilage and therefore rely on inhaled air to support their shape. As the passageways decrease in diameter, the relative amount of smooth muscle increases.

The **terminal bronchioles** subdivide into microscopic branches called respiratory bronchioles. The respiratory bronchioles subdivide into several alveolar ducts. Numerous alveoli and alveolar sacs surround the alveolar ducts. The alveolar sacs resemble bunches of grapes tethered to the end of the bronchioles ([link]). In the acinar region, the **alveolar ducts** are attached to the end of each bronchiole. At the end of each duct are approximately 100 **alveolar sacs**, each containing 20 to 30 **alveoli** that are 200 to 300 microns in diameter. Gas exchange occurs only in alveoli. Alveoli are made of thin-walled parenchymal cells, typically one-cell thick, that look like tiny bubbles within the sacs. Alveoli are in direct contact with capillaries (one-cell thick) of the circulatory system. Such intimate contact ensures that oxygen will diffuse from alveoli into the blood and be distributed to the cells of the body. In addition, the carbon dioxide that was produced by cells as a waste product will diffuse from the blood into alveoli to be exhaled. The anatomical arrangement of capillaries and alveoli emphasizes the structural and functional relationship of the respiratory and circulatory systems. Because there are so many alveoli (~300 million per lung) within each alveolar sac and so many sacs at the end of each alveolar duct, the lungs have a sponge-like consistency. This organization produces a very large surface area that is available for gas exchange. The surface area of alveoli in the lungs is approximately 75 m^2. This large surface area,

combined with the thin-walled nature of the alveolar parenchymal cells, allows gases to easily diffuse across the cells.
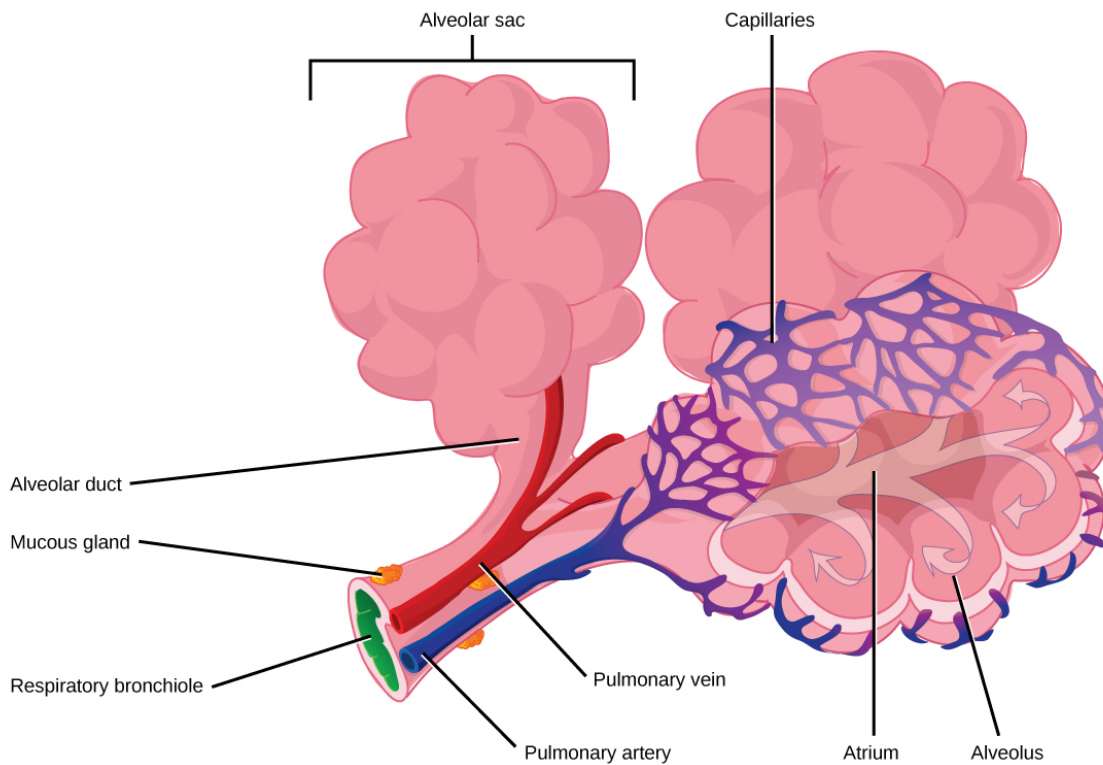
Terminal bronchioles are connected by respiratory bronchioles to alveolar ducts and alveolar sacs. Each alveolar sac contains 20 to 30 spherical alveoli and has the appearance of a bunch of grapes. Air flows into the atrium of the alveolar sac, then circulates into alveoli where gas exchange occurs with the capillaries. Mucous glands secrete mucous into the airways, keeping them moist and flexible. (credit: modification of work by Mariana Ruiz Villareal)

Note:
Link to Learning

Watch the following video to review the respiratory system. https://www.openstaxcollege.org/l/lungs_pulmonary

Protective Mechanisms

The air that organisms breathe contains **particulate matter** such as dust, dirt, viral particles, and bacteria that can damage the lungs or trigger allergic immune responses. The respiratory system contains several protective mechanisms to avoid problems or tissue damage. In the nasal cavity, hairs and mucus trap small particles, viruses, bacteria, dust, and dirt to prevent their entry.

If particulates do make it beyond the nose, or enter through the mouth, the bronchi and bronchioles of the lungs also contain several protective devices. The lungs produce **mucus**—a sticky substance made of **mucin**, a complex glycoprotein, as well as salts and water—that traps particulates. The bronchi and bronchioles contain cilia, small hair-like projections that line the walls of the bronchi and bronchioles ([link]). These cilia beat in unison and move mucus and particles out of the bronchi and bronchioles back up to the throat where it is swallowed and eliminated via the esophagus.

In humans, for example, tar and other substances in cigarette smoke destroy or paralyze the cilia, making the removal of particles more difficult. In addition, smoking causes the lungs to produce more mucus, which the damaged cilia are not able to move. This causes a persistent cough, as the lungs try to rid themselves of particulate matter, and makes smokers more susceptible to respiratory ailments.
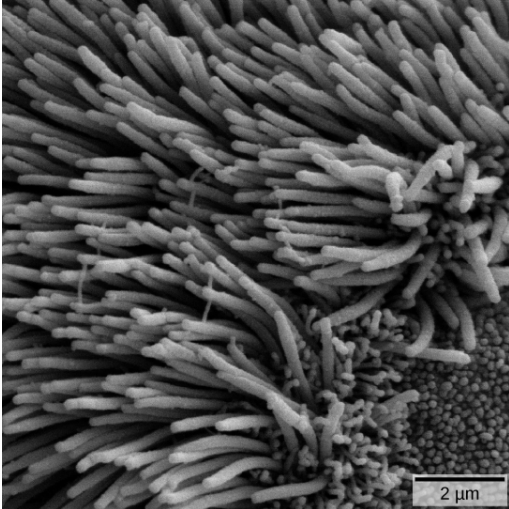
The bronchi and bronchioles contain cilia that help move mucus and other particles out of the lungs. (credit: Louisa Howard, modification of work by Dartmouth Electron Microscope Facility)

Section Summary

Animal respiratory systems are designed to facilitate gas exchange. In mammals, air is warmed and humidified in the nasal cavity. Air then travels down the pharynx, through the trachea, and into the lungs. In the lungs, air passes through the branching bronchi, reaching the respiratory bronchioles, which house the first site of gas exchange. The respiratory bronchioles open into the alveolar ducts, alveolar sacs, and alveoli. Because there are so many alveoli and alveolar sacs in the lung, the surface area for gas exchange is very large. Several protective mechanisms are in place to prevent damage or infection. These include the hair and mucus in the nasal cavity that trap dust, dirt, and other particulate matter before they can enter

the system. In the lungs, particles are trapped in a mucus layer and transported via cilia up to the esophageal opening at the top of the trachea to be swallowed.

Exercise:

Problem:

[link] Which of the following statements about the mammalian respiratory system is false?

    a. When we breathe in, air travels from the pharynx to the trachea.
    b. The bronchioles branch into bronchi.
    c. Alveolar ducts connect to alveolar sacs.
    d. Gas exchange between the lung and blood takes place in the alveolus.

Solution:

[link] B

Review Questions

Exercise:

Problem: The respiratory system _____.

    a. provides body tissues with oxygen
    b. provides body tissues with oxygen and carbon dioxide
    c. establishes how many breaths are taken per minute
    d. provides the body with carbon dioxide

Solution:

A

Exercise:

Problem:

Air is warmed and humidified in the nasal passages. This helps to
_____.

    a. ward off infection
    b. decrease sensitivity during breathing
    c. prevent damage to the lungs
    d. all of the above

Solution:

  C

Exercise:

Problem: Which is the order of airflow during inhalation?

    a. nasal cavity, trachea, larynx, bronchi, bronchioles, alveoli
    b. nasal cavity, larynx, trachea, bronchi, bronchioles, alveoli
    c. nasal cavity, larynx, trachea, bronchioles, bronchi, alveoli
    d. nasal cavity, trachea, larynx, bronchi, bronchioles, alveoli

---

Solution:

  B

Free Response

Exercise:

Problem:

Describe the function of these terms and describe where they are
located: main bronchus, trachea, alveoli, and acinus.

Solution:

The main bronchus is the conduit in the lung that funnels air to the airways where gas exchange occurs. The main bronchus attaches the lungs to the very end of the trachea where it bifurcates. The trachea is the cartilaginous structure that extends from the pharynx to the primary bronchi. It serves to funnel air to the lungs. The alveoli are the sites of gas exchange; they are located at the terminal regions of the lung and are attached to the respiratory bronchioles. The acinus is the structure in the lung where gas exchange occurs.

Exercise:

Problem: How does the structure of alveoli maximize gas exchange?

Solution:

The sac-like structure of the alveoli increases their surface area. In addition, the alveoli are made of thin-walled parenchymal cells. These features allow gases to easily diffuse across the cells.

Glossary

alveolar duct
>   duct that extends from the terminal bronchiole to the alveolar sac

alveolar sac
>   structure consisting of two or more alveoli that share a common opening

alveolus
>   (plural: alveoli) (also, air sac) terminal region of the lung where gas exchange occurs

bronchus
>   (plural: bronchi) smaller branch of cartilaginous tissue that stems off of the trachea; air is funneled through the bronchi to the region where gas

exchange occurs in alveoli

bronchiole
　　airway that extends from the main tertiary bronchi to the alveolar sac

diaphragm
　　domed-shaped skeletal muscle located under lungs that separates the
　　thoracic cavity from the abdominal cavity

larynx
　　voice box, a short passageway connecting the pharynx and the trachea

mucin
　　complex glycoprotein found in mucus

mucus
　　sticky protein-containing fluid secretion in the lung that traps
　　particulate matter to be expelled from the body

nasal cavity
　　opening of the respiratory system to the outside environment

particulate matter
　　small particle such as dust, dirt, viral particles, and bacteria that are in
　　the air

pharynx
　　throat; a tube that starts in the internal nares and runs partway down
　　the neck, where it opens into the esophagus and the larynx

primary bronchus
　　(also, main bronchus) region of the airway within the lung that
　　attaches to the trachea and bifurcates to each lung where it branches
　　into secondary bronchi

respiratory bronchiole
　　terminal portion of the bronchiole tree that is attached to the terminal
　　bronchioles and alveoli ducts, alveolar sacs, and alveoli

terminal bronchiole
> region of bronchiole that attaches to the respiratory bronchioles

trachea
> cartilaginous tube that transports air from the larynx to the primary bronchi

Gas Exchange across Respiratory Surfaces
By the end of this section, you will be able to:

- Name and describe lung volumes and capacities
- Understand how gas pressure influences how gases move into and out of the body

The structure of the lung maximizes its surface area to increase gas diffusion. Because of the enormous number of alveoli (approximately 300 million in each human lung), the surface area of the lung is very large (75 m^2). Having such a large surface area increases the amount of gas that can diffuse into and out of the lungs.

Basic Principles of Gas Exchange

Gas exchange during respiration occurs primarily through diffusion. Diffusion is a process in which transport is driven by a concentration gradient. Gas molecules move from a region of high concentration to a region of low concentration. Blood that is low in oxygen concentration and high in carbon dioxide concentration undergoes gas exchange with air in the lungs. The air in the lungs has a higher concentration of oxygen than that of oxygen-depleted blood and a lower concentration of carbon dioxide. This concentration gradient allows for gas exchange during respiration.

Partial pressure is a measure of the concentration of the individual components in a mixture of gases. The total pressure exerted by the mixture is the sum of the partial pressures of the components in the mixture. The rate of diffusion of a gas is proportional to its partial pressure within the total gas mixture. This concept is discussed further in detail below.

Lung Volumes and Capacities

Different animals have different lung capacities based on their activities. Cheetahs have evolved a much higher lung capacity than humans; it helps provide oxygen to all the muscles in the body and allows them to run very fast. Elephants also have a high lung capacity. In this case, it is not because they run fast but because they have a large body and must be able to take up oxygen in accordance with their body size.

Human lung size is determined by genetics, sex, and height. At maximal capacity, an average lung can hold almost six liters of air, but lungs do not usually operate at maximal capacity. Air in the lungs is measured in terms of **lung volumes** and **lung capacities** ([link] and [link]). Volume measures the amount of air for one function (such as inhalation or exhalation). Capacity is any two or more volumes (for example, how much can be inhaled from the end of a maximal exhalation).
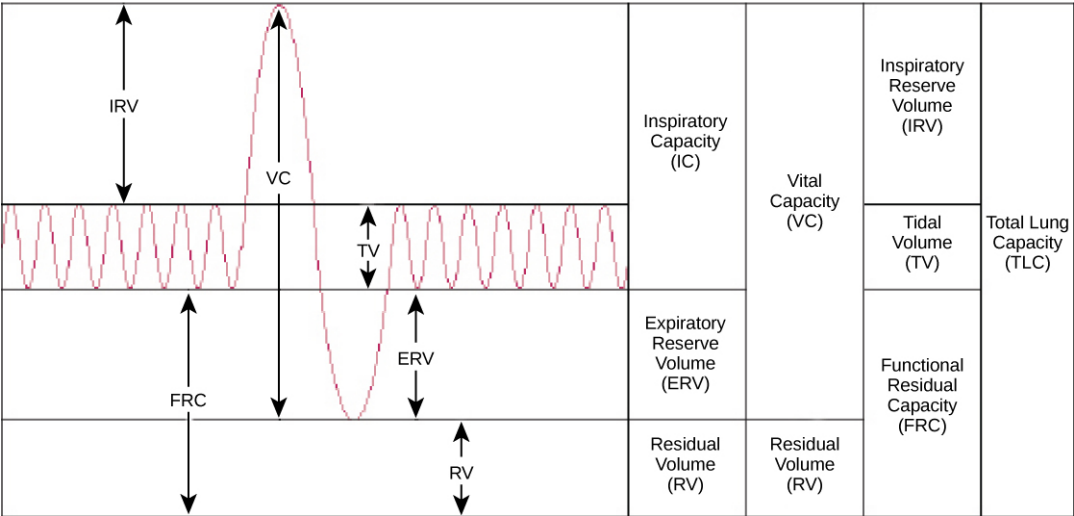
Human lung volumes and capacities are shown. The total lung capacity of the adult male is six liters. Tidal volume is the volume of air inhaled in a single, normal breath. Inspiratory capacity is the amount of air taken in during a deep breath, and residual volume is the amount of air left in the lungs after forceful respiration.

Lung Volumes and Capacities (Avg Adult Male)

Lung Volumes and Capacities (Avg Adult Male)			
Volume/Capacity	Definition	Volume (liters)	Equations
Tidal volume (TV)	Amount of air inhaled during a normal breath	0.5	-
Expiratory reserve volume (ERV)	Amount of air that can be exhaled after a normal exhalation	1.2	-
Inspiratory reserve volume (IRV)	Amount of air that can be further inhaled after a normal inhalation	3.1	-
Residual volume (RV)	Air left in the lungs after a forced exhalation	1.2	-

Lung Volumes and Capacities (Avg Adult Male)

Volume/Capacity	Definition	Volume (liters)	Equations
Vital capacity (VC)	Maximum amount of air that can be moved in or out of the lungs in a single respiratory cycle	4.8	ERV+TV+IRV
Inspiratory capacity (IC)	Volume of air that can be inhaled in addition to a normal exhalation	3.6	TV+IRV
Functional residual capacity (FRC)	Volume of air remaining after a normal exhalation	2.4	ERV+RV

Lung Volumes and Capacities (Avg Adult Male)

Volume/Capacity	Definition	Volume (liters)	Equations
Total lung capacity (TLC)	Total volume of air in the lungs after a maximal inspiration	6.0	RV+ERV+TV+IRV
Forced expiratory volume (FEV1)	How much air can be forced out of the lungs over a specific time period, usually one second	~4.1 to 5.5	-

The volume in the lung can be divided into four units: tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume. **Tidal volume (TV)** measures the amount of air that is inspired and expired during a normal breath. On average, this volume is around one-half liter, which is a little less than the capacity of a 20-ounce drink bottle. The **expiratory reserve volume (ERV)** is the additional amount of air that can be exhaled after a normal exhalation. It is the reserve amount that can be exhaled beyond what is normal. Conversely, the **inspiratory reserve volume (IRV)** is the additional amount of air that can be inhaled after a normal inhalation. The **residual volume (RV)** is the amount of air that is left after expiratory reserve volume is exhaled. The lungs are never completely empty: There is always

some air left in the lungs after a maximal exhalation. If this residual volume did not exist and the lungs emptied completely, the lung tissues would stick together and the energy necessary to re-inflate the lung could be too great to overcome. Therefore, there is always some air remaining in the lungs. Residual volume is also important for preventing large fluctuations in respiratory gases (O_2 and CO_2). The residual volume is the only lung volume that cannot be measured directly because it is impossible to completely empty the lung of air. This volume can only be calculated rather than measured.

Capacities are measurements of two or more volumes. The **vital capacity (VC)** measures the maximum amount of air that can be inhaled or exhaled during a respiratory cycle. It is the sum of the expiratory reserve volume, tidal volume, and inspiratory reserve volume. The **inspiratory capacity (IC)** is the amount of air that can be inhaled after the end of a normal expiration. It is, therefore, the sum of the tidal volume and inspiratory reserve volume. The **functional residual capacity (FRC)** includes the expiratory reserve volume and the residual volume. The FRC measures the amount of additional air that can be exhaled after a normal exhalation. Lastly, the **total lung capacity (TLC)** is a measurement of the total amount of air that the lung can hold. It is the sum of the residual volume, expiratory reserve volume, tidal volume, and inspiratory reserve volume.

Lung volumes are measured by a technique called **spirometry**. An important measurement taken during spirometry is the **forced expiratory volume (FEV)**, which measures how much air can be forced out of the lung over a specific period, usually one second (FEV1). In addition, the forced vital capacity (FVC), which is the total amount of air that can be forcibly exhaled, is measured. The ratio of these values (**FEV1/FVC ratio**) is used to diagnose lung diseases including asthma, emphysema, and fibrosis. If the FEV1/FVC ratio is high, the lungs are not compliant (meaning they are stiff and unable to bend properly), and the patient most likely has lung fibrosis. Patients exhale most of the lung volume very quickly. Conversely, when the FEV1/FVC ratio is low, there is resistance in the lung that is characteristic of asthma. In this instance, it is hard for the patient to get the air out of his or her lungs, and it takes a long time to reach the maximal exhalation volume. In either case, breathing is difficult and complications arise.

Respiratory Therapist

Respiratory therapists or respiratory practitioners evaluate and treat patients with lung and cardiovascular diseases. They work as part of a medical team to develop treatment plans for patients. Respiratory therapists may treat premature babies with underdeveloped lungs, patients with chronic conditions such as asthma, or older patients suffering from lung disease such as emphysema and chronic obstructive pulmonary disease (COPD). They may operate advanced equipment such as compressed gas delivery systems, ventilators, blood gas analyzers, and resuscitators. Specialized programs to become a respiratory therapist generally lead to a bachelor's degree with a respiratory therapist specialty. Because of a growing aging population, career opportunities as a respiratory therapist are expected to remain strong.

Gas Pressure and Respiration

The respiratory process can be better understood by examining the properties of gases. Gases move freely, but gas particles are constantly hitting the walls of their vessel, thereby producing gas pressure.

Air is a mixture of gases, primarily nitrogen (N_2; 78.6 percent), oxygen (O_2; 20.9 percent), water vapor (H_2O; 0.5 percent), and carbon dioxide (CO_2; 0.04 percent). Each gas component of that mixture exerts a pressure. The pressure for an individual gas in the mixture is the partial pressure of that gas. Approximately 21 percent of atmospheric gas is oxygen. Carbon dioxide, however, is found in relatively small amounts, 0.04 percent. The partial pressure for oxygen is much greater than that of carbon dioxide. The partial pressure of any gas can be calculated by:
Equation:

$$\mathbf{P} = (\mathbf{P}_{\text{atm}}) \times (\text{percent content in mixture}).$$

P_{atm}, the atmospheric pressure, is the sum of all of the partial pressures of the atmospheric gases added together,
Equation:

$$P_{atm} = P_{N_2} + P_{O_2} + P_{H_2O} + P_{CO_2} = 760 \text{ mm Hg}$$

$\times$ (percent content in mixture).

The pressure of the atmosphere at sea level is 760 mm Hg. Therefore, the partial pressure of oxygen is:
Equation:

$$P_{O_2} = (760 \text{ mm Hg}) \, (0.21) = 160 \text{ mm Hg}$$

and for carbon dioxide:
Equation:

$$P_{CO_2} = (760 \text{ mm Hg}) \, (0.0004) = 0.3 \text{ mm Hg}.$$

At high altitudes, P_{atm} decreases but concentration does not change; the partial pressure decrease is due to the reduction in P_{atm}.

When the air mixture reaches the lung, it has been humidified. The pressure of the water vapor in the lung does not change the pressure of the air, but it must be included in the partial pressure equation. For this calculation, the water pressure (47 mm Hg) is subtracted from the atmospheric pressure:
Equation:

$$760 \text{ mm Hg} \, - \, 47 \text{ mm Hg} \, = \, 713 \text{ mm Hg}$$

and the partial pressure of oxygen is:
Equation:

$$(760 \text{ mm Hg} \, - \, 47 \text{ mm Hg}) \, \times \, 0.21 \, = \, 150 \text{ mm Hg}.$$

These pressures determine the gas exchange, or the flow of gas, in the system. Oxygen and carbon dioxide will flow according to their pressure gradient from high to low. Therefore, understanding the partial pressure of each gas will aid in understanding how gases move in the respiratory system.

Gas Exchange across the Alveoli

In the body, oxygen is used by cells of the body's tissues and carbon dioxide is produced as a waste product. The ratio of carbon dioxide production to oxygen consumption is the **respiratory quotient (RQ)**. RQ varies between 0.7 and 1.0. If just glucose were used to fuel the body, the RQ would equal one. One mole of carbon dioxide would be produced for every mole of oxygen consumed. Glucose, however, is not the only fuel for the body. Protein and fat are also used as fuels for the body. Because of this, less carbon dioxide is produced than oxygen is consumed and the RQ is, on average, about 0.7 for fat and about 0.8 for protein.

The RQ is used to calculate the partial pressure of oxygen in the alveolar spaces within the lung, the **alveolar** P_{O_2} Above, the partial pressure of oxygen in the lungs was calculated to be 150 mm Hg. However, lungs never fully deflate with an exhalation; therefore, the inspired air mixes with this residual air and lowers the partial pressure of oxygen within the alveoli. This means that there is a lower concentration of oxygen in the lungs than is found in the air outside the body. Knowing the RQ, the partial pressure of oxygen in the alveoli can be calculated:
Equation:

$$\text{alveolar } P_{O_2} = \text{inspired } P_{O_2} - \left(\frac{\text{alveolar } P_{O_2}}{RQ} \right)$$

With an RQ of 0.8 and a P_{CO_2} in the alveoli of 40 mm Hg, the alveolar P_{O_2} is equal to:
Equation:

$$\text{alveolar } P_{O_2} = 150 \text{ mm Hg} - \left(\frac{40 \text{ mm Hg}}{0.8} \right) = \text{ mm Hg.}$$

Notice that this pressure is less than the external air. Therefore, the oxygen will flow from the inspired air in the lung (P_{O_2} = 150 mm Hg) into the bloodstream (P_{O_2} = 100 mm Hg) ([link]).

In the lungs, oxygen diffuses out of the alveoli and into the capillaries surrounding the alveoli. Oxygen (about 98 percent) binds reversibly to the respiratory pigment hemoglobin found in red blood cells (RBCs). RBCs carry oxygen to the tissues where oxygen dissociates from the hemoglobin and diffuses into the cells of the tissues. More specifically, alveolar P_{O_2} is higher in the alveoli (P_{ALVO_2} = 100 mm Hg) than blood P_{O_2} (40 mm Hg) in the capillaries. Because this pressure gradient exists, oxygen diffuses down its pressure gradient, moving out of the alveoli and entering the blood of the capillaries where O_2 binds to hemoglobin. At the same time, alveolar P_{CO_2} is lower P_{ALVO_2} = 40 mm Hg than blood P_{CO_2} = (45 mm Hg). CO_2 diffuses down its pressure gradient, moving out of the capillaries and entering the alveoli.

Oxygen and carbon dioxide move independently of each other; they diffuse down their own pressure gradients. As blood leaves the lungs through the pulmonary veins, the **venous** P_{O_2}= 100 mm Hg, whereas the **venous** P_{CO_2} = 40 mm Hg. As blood enters the systemic capillaries, the blood will lose oxygen and gain carbon dioxide because of the pressure difference of the tissues and blood. In systemic capillaries, P_{O_2}= 100 mm Hg, but in the tissue cells, P_{O_2}= 40 mm Hg. This pressure gradient drives the diffusion of oxygen out of the capillaries and into the tissue cells. At the same time, blood P_{CO_2}= 40 mm Hg and systemic tissue P_{CO_2}= 45 mm Hg. The pressure gradient drives CO_2 out of tissue cells and into the capillaries. The blood returning to the lungs through the pulmonary arteries has a venous P_{O_2}= 40 mm Hg and a P_{CO_2}= 45 mm Hg. The blood enters the lung capillaries where the process of exchanging gases between the capillaries and alveoli begins again ([link]).

Note:
Art Connection
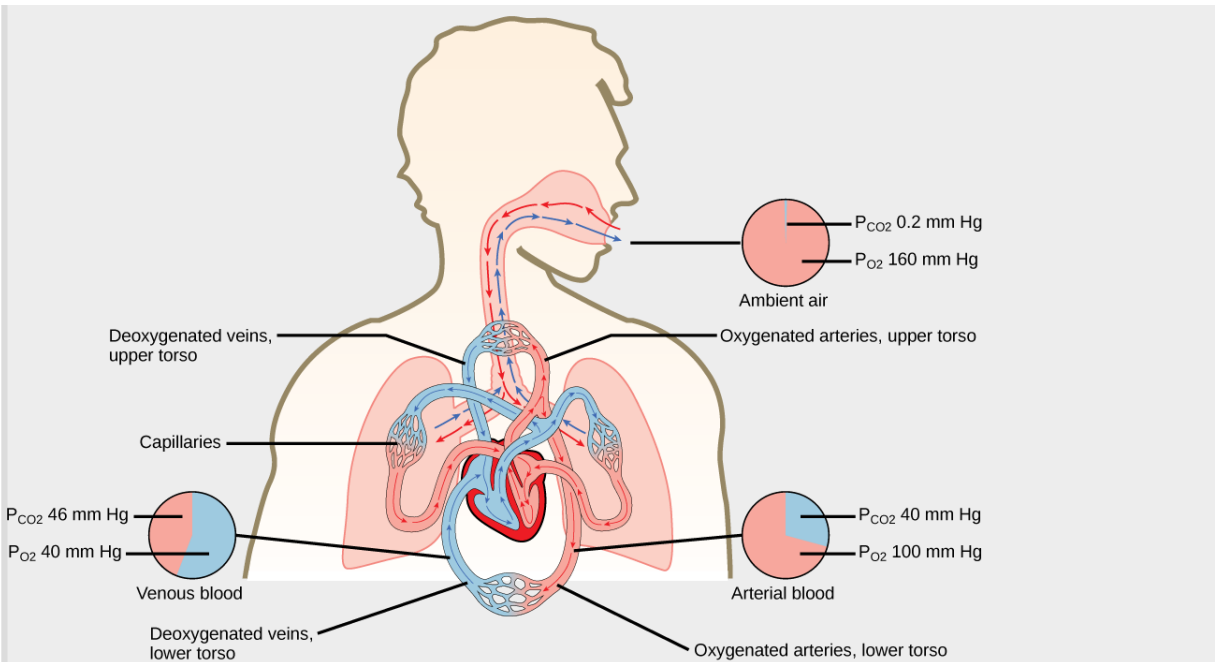
The partial pressures of oxygen and carbon dioxide
change as blood moves through the body.

Which of the following statements is false?

a. In the tissues, P_{O_2} drops as blood passes from the arteries to the veins, while P_{CO_2} increases.
b. Blood travels from the lungs to the heart to body tissues, then back to the heart, then the lungs.
c. Blood travels from the lungs to the heart to body tissues, then back to the lungs, then the heart.
d. P_{O_2} is higher in air than in the lungs.

In short, the change in partial pressure from the alveoli to the capillaries drives the oxygen into the tissues and the carbon dioxide into the blood from the tissues. The blood is then transported to the lungs where differences in pressure in the alveoli result in the movement of carbon dioxide out of the blood into the lungs, and oxygen into the blood.

Section Summary

The lungs can hold a large volume of air, but they are not usually filled to maximal capacity. Lung volume measurements include tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume. The sum of these equals the total lung capacity. Gas movement into or out of the lungs is dependent on the pressure of the gas. Air is a mixture of gases; therefore, the partial pressure of each gas can be calculated to determine how the gas will flow in the lung. The difference between the partial pressure of the gas in the air drives oxygen into the tissues and carbon dioxide out of the body.

Art Connections

Exercise:

Problem: [link] Which of the following statements is false?

a. In the tissues, P_{O_2} drops as blood passes from the arteries to the veins, while P_{CO_2} increases.
b. Blood travels from the lungs to the heart to body tissues, then back to the heart, then the lungs.
c. Blood travels from the lungs to the heart to body tissues, then back to the lungs, then the heart.

d. P_{O_2} is higher in air than in the lungs.

Solution:

C

Review Questions

Exercise:

Problem: The inspiratory reserve volume measures the _____.

    a. amount of air remaining in the lung after a maximal exhalation
    b. amount of air that the lung holds
    c. amount of air the can be further exhaled after a normal breath
    d. amount of air that can be further inhaled after a normal breath

---

Solution:

D

Exercise:

Problem:

Of the following, which does not explain why the partial pressure of oxygen is lower in the lung than in the external air?

    a. Air in the lung is humidified; therefore, water vapor pressure alters the pressure.
    b. Carbon dioxide mixes with oxygen.
    c. Oxygen is moved into the blood and is headed to the tissues.
    d. Lungs exert a pressure on the air to reduce the oxygen pressure.

Solution:

D

Exercise:

Problem:

The total lung capacity is calculated using which of the following formulas?

   a. residual volume + tidal volume + inspiratory reserve volume
   b. residual volume + expiratory reserve volume + inspiratory reserve volume
   c. expiratory reserve volume + tidal volume + inspiratory reserve volume
   d. residual volume + expiratory reserve volume + tidal volume + inspiratory reserve volume

Solution:

D

Free Response

Exercise:

Problem:

What does FEV1/FVC measure? What factors may affect FEV1/FVC?

Solution:

FEV1/FVC measures the forced expiratory volume in one second in relation to the total forced vital capacity (the total amount of air that is exhaled from the lung from a maximal inhalation). This ratio changes with alterations in lung function that arise from diseases such as fibrosis, asthma, and COPD.

Exercise:

Problem: What is the reason for having residual volume in the lung?

Solution:

If all the air in the lung were exhaled, then opening the alveoli for the next inspiration would be very difficult. This is because the tissues would stick together.

Exercise:

Problem:

How can a decrease in the percent of oxygen in the air affect the movement of oxygen in the body?

Solution:

Oxygen moves from the lung to the bloodstream to the tissues according to the pressure gradient. This is measured as the partial pressure of oxygen. If the amount of oxygen drops in the inspired air, there would be reduced partial pressure. This would decrease the driving force that moves the oxygen into the blood and into the tissues. P_{O_2} is also reduced at high elevations: P_{O_2} at high elevations is lower than at sea level because the total atmospheric pressure is less than atmospheric pressure at sea level.

Exercise:

Problem:

If a patient has increased resistance in his or her lungs, how can this detected by a doctor? What does this mean?

Solution:

A doctor can detect a restrictive disease using spirometry. By detecting the rate at which air can be expelled from the lung, a diagnosis of fibrosis or another restrictive disease can be made.

Glossary

alveolar P_{O_2}
 partial pressure of oxygen in the alveoli (usually around 100 mmHg)

expiratory reserve volume (ERV)
 amount of additional air that can be exhaled after a normal exhalation

FEV1/FVC ratio
 ratio of how much air can be forced out of the lung in one second to the
 total amount that is forced out of the lung; a measurement of lung
 function that can be used to detect disease states

forced expiratory volume (FEV)
 (also, forced vital capacity) measure of how much air can be forced out
 of the lung from maximal inspiration over a specific amount of time

functional residual capacity (FRC)
 expiratory reserve volume plus residual volume

inspiratory capacity (IC)
 tidal volume plus inspiratory reserve volume

inspiratory reserve volume (IRV)
 amount of additional air that can be inspired after a normal inhalation

lung capacity
 measurement of two or more lung volumes (how much air can be inhaled
 from the end of an expiration to maximal capacity)

lung volume
 measurement of air for one lung function (normal inhalation or
 exhalation)

partial pressure
 amount of pressure exerted by one gas within a mixture of gases

residual volume (RV)
 amount of air remaining in the lung after a maximal expiration

respiratory quotient (RQ)

ratio of carbon dioxide production to each oxygen molecule consumed

spirometry

method to measure lung volumes and to diagnose lung diseases

tidal volume (TV)

amount of air that is inspired and expired during normal breathing

total lung capacity (TLC)

sum of the residual volume, expiratory reserve volume, tidal volume, and inspiratory reserve volume

venous P_{CO_2}

partial pressure of carbon dioxide in the veins (40 mm Hg in the pulmonary veins)

venous P_{O_2}

partial pressure of oxygen in the veins (100 mm Hg in the pulmonary veins)

vital capacity (VC)

sum of the expiratory reserve volume, tidal volume, and inspiratory reserve volume

Breathing
By the end of this section, you will be able to:

- Describe how the structures of the lungs and thoracic cavity control the mechanics of breathing
- Explain the importance of compliance and resistance in the lungs
- Discuss problems that may arise due to a V/Q mismatch

Mammalian lungs are located in the thoracic cavity where they are surrounded and protected by the rib cage, intercostal muscles, and bound by the chest wall. The bottom of the lungs is contained by the diaphragm, a skeletal muscle that facilitates breathing. Breathing requires the coordination of the lungs, the chest wall, and most importantly, the diaphragm.

Types of Breathing

Amphibians have evolved multiple ways of breathing. Young amphibians, like tadpoles, use gills to breathe, and they don't leave the water. Some amphibians retain gills for life. As the tadpole grows, the gills disappear and lungs grow. These lungs are primitive and not as evolved as mammalian lungs. Adult amphibians are lacking or have a reduced diaphragm, so breathing via lungs is forced. The other means of breathing for amphibians is diffusion across the skin. To aid this diffusion, amphibian skin must remain moist.

Birds face a unique challenge with respect to breathing: They fly. Flying consumes a great amount of energy; therefore, birds require a lot of oxygen to aid their metabolic processes. Birds have evolved a respiratory system that supplies them with the oxygen needed to enable flying. Similar to mammals, birds have lungs, which are organs specialized for gas exchange. Oxygenated air, taken in during inhalation, diffuses across the surface of the lungs into the bloodstream, and carbon dioxide diffuses from the blood into the lungs and expelled during exhalation. The details of breathing between birds and mammals differ substantially.

In addition to lungs, birds have air sacs inside their body. Air flows in one direction from the posterior air sacs to the lungs and out of the anterior air sacs. The flow of air is in the opposite direction from blood flow, and gas exchange takes place much more efficiently. This type of breathing enables birds to obtain the requisite oxygen, even at higher altitudes where the oxygen concentration is low. This directionality of airflow requires two cycles of air intake and exhalation to completely get the air out of the lungs.

Note:
Evolution Connection
Avian Respiration
Birds have evolved a respiratory system that enables them to fly. Flying is a high-energy process and requires a lot of oxygen. Furthermore, many birds fly in high altitudes where the concentration of oxygen in low. How did birds evolve a respiratory system that is so unique?
Decades of research by paleontologists have shown that birds evolved from therapods, meat-eating dinosaurs ([link]). In fact, fossil evidence shows that meat-eating dinosaurs that lived more than 100 million years ago had a similar flow-through respiratory system with lungs and air sacs. *Archaeopteryx* and *Xiaotingia*, for example, were flying dinosaurs and are believed to be early precursors of birds.
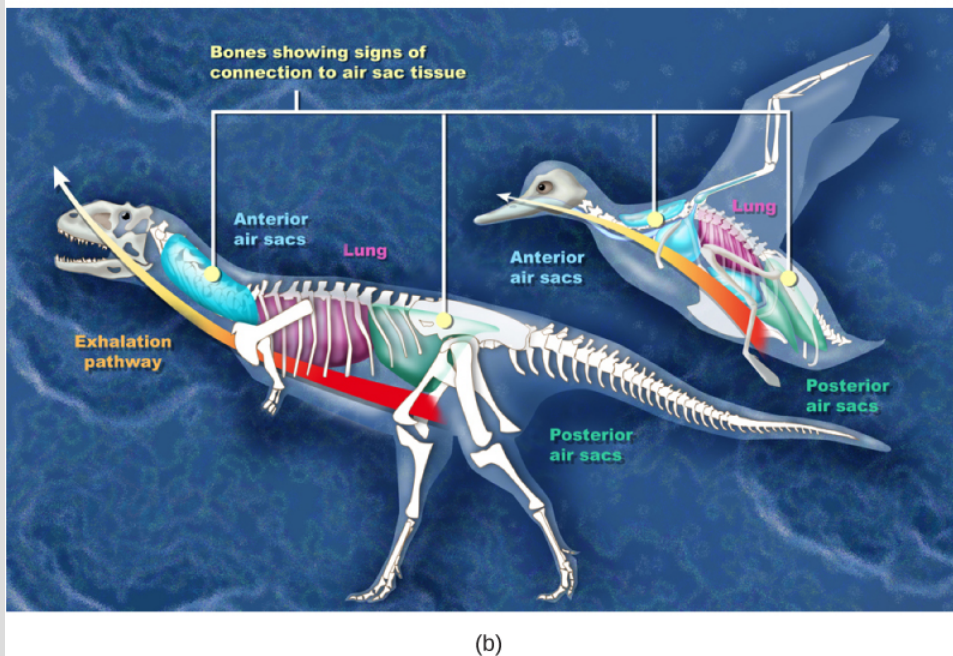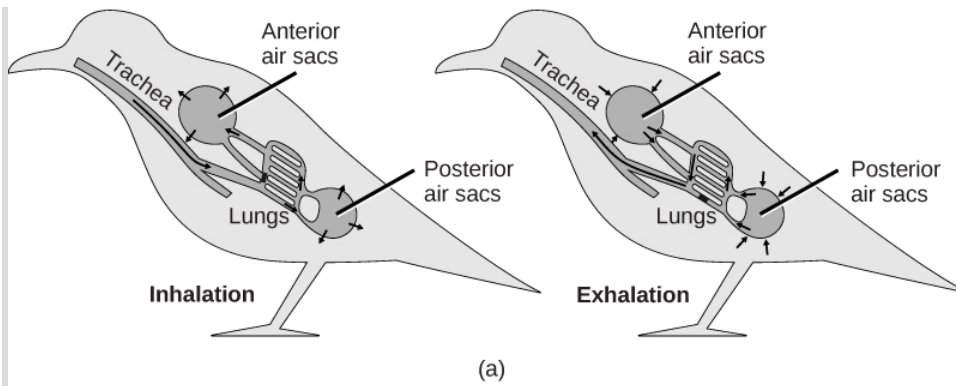
(a) Birds have a flow-through respiratory system in which air flows unidirectionally from the posterior sacs into the lungs, then into the anterior air sacs. The air sacs connect to openings in hollow bones. (b) Dinosaurs, from which birds descended, have similar hollow bones and are believed to have had a similar respiratory system. (credit b: modification of work by Zina Deretsky, National Science Foundation)

Most of us consider that dinosaurs are extinct. However, modern birds are descendants of avian dinosaurs. The respiratory system of modern birds has been evolving for hundreds of millions of years.

All mammals have lungs that are the main organs for breathing. Lung capacity has evolved to support the animal's activities. During inhalation, the lungs expand with air, and oxygen diffuses across the lung's surface and enters the bloodstream. During exhalation, the lungs expel air and lung volume decreases. In the next few sections, the process of human breathing will be explained.

The Mechanics of Human Breathing

Boyle's Law is the gas law that states that in a closed space, pressure and volume are inversely related. As volume decreases, pressure increases and vice versa ([link]). The relationship between gas pressure and volume helps to explain the mechanics of breathing.
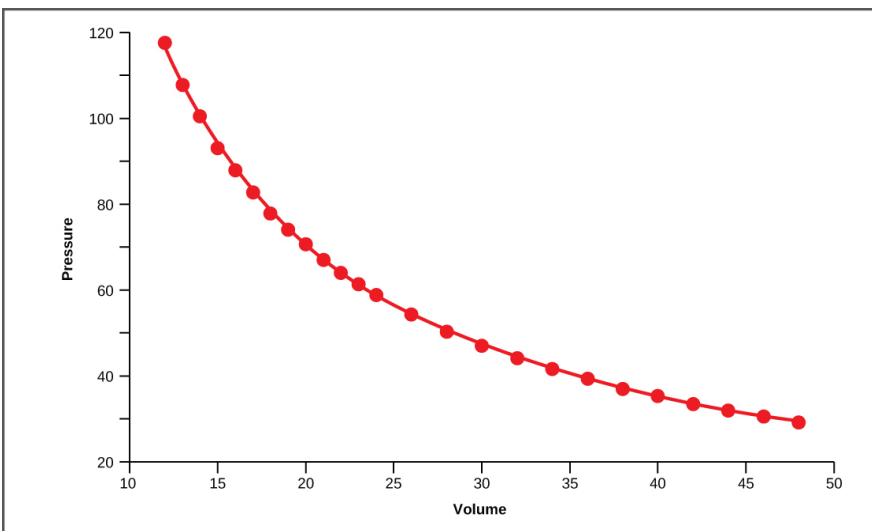
This graph shows data from Boyle's original 1662 experiment, which shows that pressure and volume are inversely related. No units are given as Boyle used arbitrary units in his experiments.

There is always a slightly negative pressure within the thoracic cavity, which aids in keeping the airways of the lungs open. During inhalation, volume increases as a result of contraction of the diaphragm, and pressure decreases (according to Boyle's Law). This decrease of pressure in the thoracic cavity relative to the environment makes the cavity less than the atmosphere ([link]**a**). Because of this drop in pressure, air rushes into the respiratory passages. To increase the volume of the lungs, the chest wall expands. This results from the contraction of the **intercostal muscles**, the muscles that are connected to the rib cage. Lung volume expands because the diaphragm contracts and the intercostals muscles contract, thus expanding the thoracic cavity. This increase in the volume of the thoracic cavity lowers pressure compared to the atmosphere, so air rushes into the lungs, thus increasing its volume. The resulting increase in volume is largely attributed to an increase in alveolar space, because the bronchioles and bronchi are stiff structures that do not change in size.

Inhalation
(a)
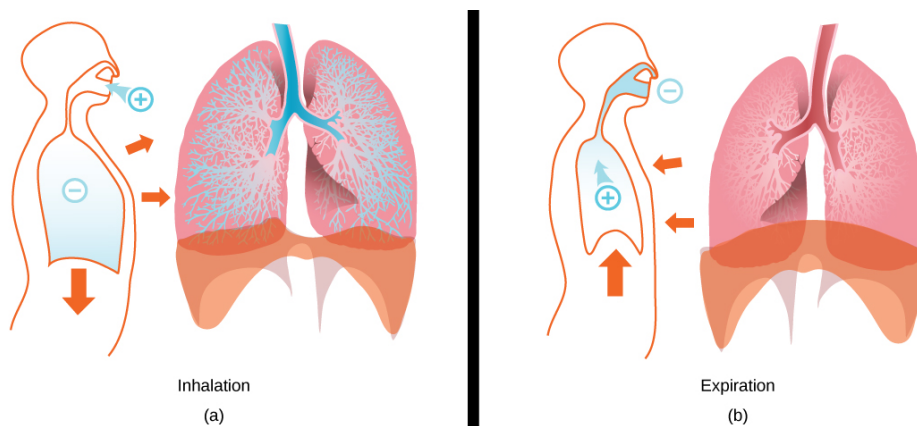
Expiration
(b)

The lungs, chest wall, and diaphragm are all involved in respiration, both (a) inhalation and (b) expiration. (credit: modification of work by Mariana Ruiz Villareal)

The chest wall expands out and away from the lungs. The lungs are elastic; therefore, when air fills the lungs, the **elastic recoil** within the tissues of the lung exerts pressure back toward the interior of the lungs. These outward

and inward forces compete to inflate and deflate the lung with every breath. Upon exhalation, the lungs recoil to force the air out of the lungs, and the intercostal muscles relax, returning the chest wall back to its original position ([link]**b**). The diaphragm also relaxes and moves higher into the thoracic cavity. This increases the pressure within the thoracic cavity relative to the environment, and air rushes out of the lungs. The movement of air out of the lungs is a passive event. No muscles are contracting to expel the air.

Each lung is surrounded by an invaginated sac. The layer of tissue that covers the lung and dips into spaces is called the visceral **pleura**. A second layer of parietal pleura lines the interior of the thorax ([link]). The space between these layers, the **intrapleural space**, contains a small amount of fluid that protects the tissue and reduces the friction generated from rubbing the tissue layers together as the lungs contract and relax. **Pleurisy** results when these layers of tissue become inflamed; it is painful because the inflammation increases the pressure within the thoracic cavity and reduces the volume of the lung.
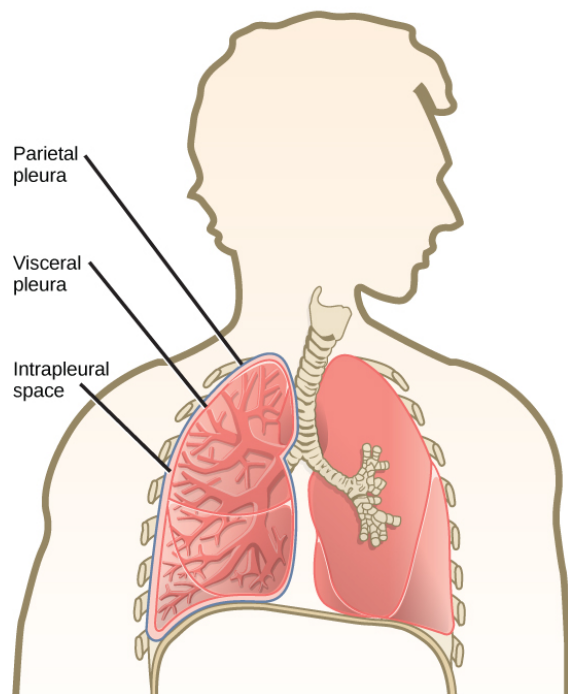
A tissue layer called pleura surrounds the lung and interior of the thoracic cavity. (credit: modification of work by NCI)

The Work of Breathing

The number of breaths per minute is the **respiratory rate**. On average, under non-exertion conditions, the human respiratory rate is 12–15 breaths/minute. The respiratory rate contributes to the **alveolar ventilation**, or how much air moves into and out of the alveoli. Alveolar ventilation prevents carbon dioxide buildup in the alveoli. There are two ways to keep the alveolar ventilation constant: increase the respiratory rate while decreasing the tidal volume of air per breath (shallow breathing), or decrease the respiratory rate while increasing the tidal volume per breath. In either case, the ventilation remains the same, but the work done and type of

work needed are quite different. Both tidal volume and respiratory rate are closely regulated when oxygen demand increases.

There are two types of work conducted during respiration, flow-resistive and elastic work. **Flow-resistive** refers to the work of the alveoli and tissues in the lung, whereas **elastic work** refers to the work of the intercostal muscles, chest wall, and diaphragm. Increasing the respiration rate increases the flow-resistive work of the airways and decreases the elastic work of the muscles. Decreasing the respiratory rate reverses the type of work required.

Surfactant

The air-tissue/water interface of the alveoli has a high surface tension. This surface tension is similar to the surface tension of water at the liquid-air interface of a water droplet that results in the bonding of the water molecules together. **Surfactant** is a complex mixture of phospholipids and lipoproteins that works to reduce the surface tension that exists between the alveoli tissue and the air found within the alveoli. By lowering the surface tension of the alveolar fluid, it reduces the tendency of alveoli to collapse.

Surfactant works like a detergent to reduce the surface tension and allows for easier inflation of the airways. When a balloon is first inflated, it takes a large amount of effort to stretch the plastic and start to inflate the balloon. If a little bit of detergent was applied to the interior of the balloon, then the amount of effort or work needed to begin to inflate the balloon would decrease, and it would become much easier to start blowing up the balloon. This same principle applies to the airways. A small amount of surfactant to the airway tissues reduces the effort or work needed to inflate those airways. Babies born prematurely sometimes do not produce enough surfactant. As a result, they suffer from **respiratory distress syndrome**, because it requires more effort to inflate their lungs. Surfactant is also important for preventing collapse of small alveoli relative to large alveoli.

Lung Resistance and Compliance

Pulmonary diseases reduce the rate of gas exchange into and out of the lungs. Two main causes of decreased gas exchange are **compliance** (how elastic the lung is) and **resistance** (how much obstruction exists in the airways). A change in either can dramatically alter breathing and the ability to take in oxygen and release carbon dioxide.

Examples of **restrictive diseases** are respiratory distress syndrome and pulmonary fibrosis. In both diseases, the airways are less compliant and they are stiff or fibrotic. There is a decrease in compliance because the lung tissue cannot bend and move. In these types of restrictive diseases, the intrapleural pressure is more positive and the airways collapse upon exhalation, which traps air in the lungs. Forced or **functional vital capacity (FVC)**, which is the amount of air that can be forcibly exhaled after taking the deepest breath possible, is much lower than in normal patients, and the time it takes to exhale most of the air is greatly prolonged ([link]). A patient suffering from these diseases cannot exhale the normal amount of air.

Obstructive diseases and conditions include emphysema, asthma, and pulmonary edema. In emphysema, which mostly arises from smoking tobacco, the walls of the alveoli are destroyed, decreasing the surface area for gas exchange. The overall compliance of the lungs is increased, because as the alveolar walls are damaged, lung elastic recoil decreases due to a loss of elastic fibers, and more air is trapped in the lungs at the end of exhalation. Asthma is a disease in which inflammation is triggered by environmental factors. Inflammation obstructs the airways. The obstruction may be due to edema (fluid accumulation), smooth muscle spasms in the walls of the bronchioles, increased mucus secretion, damage to the epithelia of the airways, or a combination of these events. Those with asthma or edema experience increased occlusion from increased inflammation of the airways. This tends to block the airways, preventing the proper movement of gases ([link]). Those with obstructive diseases have large volumes of air trapped after exhalation and breathe at a very high lung volume to compensate for the lack of airway recruitment.

FEV1/FVC Ratio
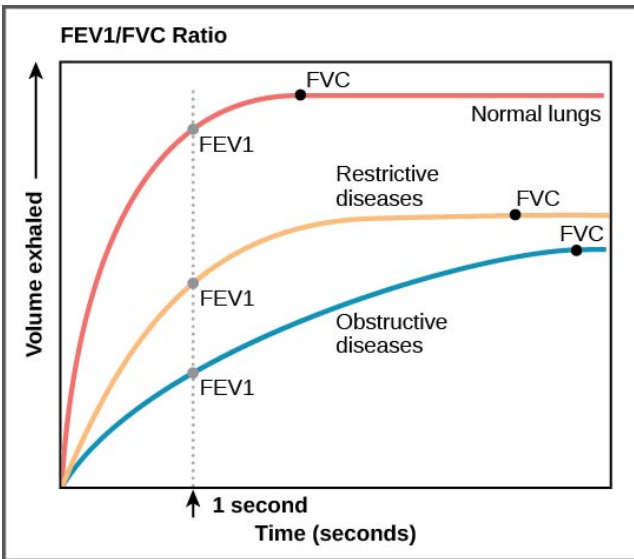
The ratio of FEV1 (the amount of air that can be forcibly exhaled in one second after taking a deep breath) to FVC (the total amount of air that can be forcibly exhaled) can be used to diagnose whether a person has restrictive or obstructive lung disease. In restrictive lung disease, FVC is reduced but airways are not obstructed, so the person is able to expel air reasonably fast. In obstructive lung disease, airway obstruction results in slow exhalation as well as reduced FVC. Thus, the FEV1/FVC ratio is lower in persons with obstructive lung disease (less than 69 percent) than in persons with restrictive disease (88 to 90 percent).

Dead Space: V/Q Mismatch

Pulmonary circulation pressure is very low compared to that of the systemic circulation. It is also independent of cardiac output. This is because of a phenomenon called **recruitment**, which is the process of opening airways that normally remain closed when cardiac output increases. As cardiac output increases, the number of capillaries and arteries that are perfused (filled with blood) increases. These capillaries and arteries are not always in use but are ready if needed. At times, however, there is a mismatch between the amount of air (ventilation, V) and the amount of blood (perfusion, Q) in the lungs. This is referred to as **ventilation/perfusion (V/Q) mismatch**.

There are two types of V/Q mismatch. Both produce **dead space**, regions of broken down or blocked lung tissue. Dead spaces can severely impact breathing, because they reduce the surface area available for gas diffusion. As a result, the amount of oxygen in the blood decreases, whereas the carbon dioxide level increases. Dead space is created when no ventilation and/or perfusion takes place. **Anatomical dead space** or anatomical shunt, arises from an anatomical failure, while **physiological dead space** or physiological shunt, arises from a functional impairment of the lung or arteries.

An example of an anatomical shunt is the effect of gravity on the lungs. The lung is particularly susceptible to changes in the magnitude and direction of gravitational forces. When someone is standing or sitting upright, the pleural pressure gradient leads to increased ventilation further down in the lung. As a result, the intrapleural pressure is more negative at the base of the lung than at the top, and more air fills the bottom of the lung than the top. Likewise, it takes less energy to pump blood to the bottom of the lung than to the top when in a prone position. Perfusion of the lung is not uniform while standing or sitting. This is a result of hydrostatic forces combined with the effect of airway pressure. An anatomical shunt develops because the ventilation of the airways does not match the perfusion of the arteries surrounding those airways. As a result, the rate of gas exchange is reduced. Note that this does not occur when lying down, because in this position, gravity does not preferentially pull the bottom of the lung down.

A physiological shunt can develop if there is infection or edema in the lung that obstructs an area. This will decrease ventilation but not affect perfusion; therefore, the V/Q ratio changes and gas exchange is affected.

The lung can compensate for these mismatches in ventilation and perfusion. If ventilation is greater than perfusion, the arterioles dilate and the bronchioles constrict. This increases perfusion and reduces ventilation. Likewise, if ventilation is less than perfusion, the arterioles constrict and the bronchioles dilate to correct the imbalance.

Section Summary

The structure of the lungs and thoracic cavity control the mechanics of breathing. Upon inspiration, the diaphragm contracts and lowers. The intercostal muscles contract and expand the chest wall outward. The intrapleural pressure drops, the lungs expand, and air is drawn into the airways. When exhaling, the intercostal muscles and diaphragm relax, returning the intrapleural pressure back to the resting state. The lungs recoil and airways close. The air passively exits the lung. There is high surface tension at the air-airway interface in the lung. Surfactant, a mixture of phospholipids and lipoproteins, acts like a detergent in the airways to reduce surface tension and allow for opening of the alveoli.

Breathing and gas exchange are both altered by changes in the compliance and resistance of the lung. If the compliance of the lung decreases, as occurs in restrictive diseases like fibrosis, the airways stiffen and collapse upon exhalation. Air becomes trapped in the lungs, making breathing more difficult. If resistance increases, as happens with asthma or emphysema, the airways become obstructed, trapping air in the lungs and causing breathing to become difficult. Alterations in the ventilation of the airways or perfusion of the arteries can affect gas exchange. These changes in ventilation and perfusion, called V/Q mismatch, can arise from anatomical or physiological changes.

Review Questions

Exercise:

Problem: How would paralysis of the diaphragm alter inspiration?

    a. It would prevent contraction of the intercostal muscles.
    b. It would prevent inhalation because the intrapleural pressure would not change.
    c. It would decrease the intrapleural pressure and allow more air to enter the lungs.
    d. It would slow expiration because the lung would not relax.

Solution:

B

Exercise:

Problem: Restrictive airway diseases _____.

    a. increase the compliance of the lung
    b. decrease the compliance of the lung
    c. increase the lung volume
    d. decrease the work of breathing

Solution:

B

Exercise:

Problem: Alveolar ventilation remains constant when _____.

    a. the respiratory rate is increased while the volume of air per breath
       is decreased
    b. the respiratory rate and the volume of air per breath are increased
    c. the respiratory rate is decreased while increasing the volume per
       breath
    d. both a and c

Solution:

D

Free Response

Exercise:

Problem:

How would increased airway resistance affect intrapleural pressure during inhalation?

Solution:

Increased airway resistance increases the volume and pressure in the lung; therefore, the intrapleural pressure would be less negative and breathing would be more difficult.

Exercise:

Problem:

Explain how a puncture to the thoracic cavity (from a knife wound, for instance) could alter the ability to inhale.

Solution:

A puncture to the thoracic cavity would equalize the pressure inside the thoracic cavity to the outside environment. For the lung to function properly, the intrapleural pressure must be negative. This is caused by the contraction of the diaphragm pulling the lungs down and drawing air into the lungs.

Exercise:

Problem:

When someone is standing, gravity stretches the bottom of the lung down toward the floor to a greater extent than the top of the lung. What implication could this have on the flow of air in the lungs? Where does gas exchange occur in the lungs?

Solution:

The lung is particularly susceptible to changes in the magnitude and direction of gravitational forces. When someone is standing or sitting upright, the pleural pressure gradient leads to increased ventilation further down in the lung.

Glossary

alveolar ventilation
    how much air is in the alveoli

anatomical dead space
    (also, anatomical shunt) region of the lung that lacks proper ventilation/perfusion due to an anatomical block

compliance
    measurement of the elasticity of the lung

dead space
    area in the lung that lacks proper ventilation or perfusion

elastic recoil
    property of the lung that drives the lung tissue inward

elastic work
    work conducted by the intercostal muscles, chest wall, and diaphragm

flow-resistive
    work of breathing performed by the alveoli and tissues in the lung

functional vital capacity (FVC)
    amount of air that can be forcibly exhaled after taking the deepest
    breath possible

intercostal muscle
    muscle connected to the rib cage that contracts upon inspiration

intrapleural space
    space between the layers of pleura

obstructive disease
    disease (such as emphysema and asthma) that arises from obstruction
    of the airways; compliance increases in these diseases

physiological dead space
    (also, physiological shunt) region of the lung that lacks proper
    ventilation/perfusion due to a physiological change in the lung (like
    inflammation or edema)

pleura
    tissue layer that surrounds the lungs and lines the interior of the
    thoracic cavity

pleurisy

painful inflammation of the pleural tissue layers

recruitment
    process of opening airways that normally remain closed when the
    cardiac output increases

resistance
    measurement of lung obstruction

respiratory distress syndrome
    disease that arises from a deficient amount of surfactant

respiratory rate
    number of breaths per minute

restrictive disease
    disease that results from a restriction and decreased compliance of the
    alveoli; respiratory distress syndrome and pulmonary fibrosis are
    examples

surfactant
    detergent-like liquid in the airways that lowers the surface tension of
    the alveoli to allow for expansion

ventilation/perfusion (V/Q) mismatch
    region of the lung that lacks proper alveolar ventilation (V) and/or
    arterial perfusion (Q)

Transport of Gases in Human Bodily Fluids
By the end of this section, you will be able to:

- Describe how oxygen is bound to hemoglobin and transported to body tissues
- Explain how carbon dioxide is transported from body tissues to the lungs

Once the oxygen diffuses across the alveoli, it enters the bloodstream and is transported to the tissues where it is unloaded, and carbon dioxide diffuses out of the blood and into the alveoli to be expelled from the body. Although gas exchange is a continuous process, the oxygen and carbon dioxide are transported by different mechanisms.

Transport of Oxygen in the Blood

Although oxygen dissolves in blood, only a small amount of oxygen is transported this way. Only 1.5 percent of oxygen in the blood is dissolved directly into the blood itself. Most oxygen—98.5 percent—is bound to a protein called hemoglobin and carried to the tissues.

Hemoglobin

Hemoglobin, or Hb, is a protein molecule found in red blood cells (erythrocytes) made of four subunits: two alpha subunits and two beta subunits ([link]). Each subunit surrounds a central **heme group** that contains iron and binds one oxygen molecule, allowing each hemoglobin molecule to bind four oxygen molecules. Molecules with more oxygen bound to the heme groups are brighter red. As a result, oxygenated arterial blood where the Hb is carrying four oxygen molecules is bright red, while venous blood that is deoxygenated is darker red.

(a) Red blood cells
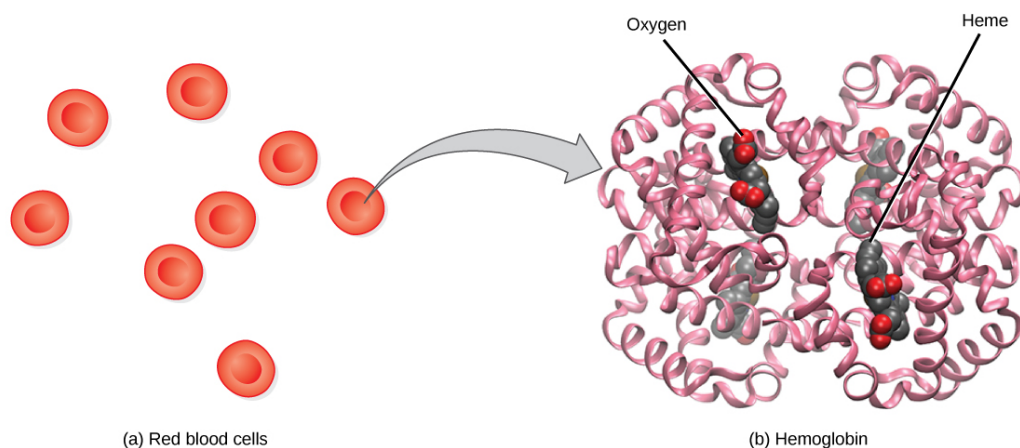
(b) Hemoglobin

The protein inside (a) red blood cells that carries oxygen to cells and carbon dioxide to the lungs is (b) hemoglobin. Hemoglobin is made up of four symmetrical subunits and four heme groups. Iron associated with the heme binds oxygen. It is the iron in hemoglobin that gives blood its red color.

It is easier to bind a second and third oxygen molecule to Hb than the first molecule. This is because the hemoglobin molecule changes its shape, or conformation, as oxygen binds. The fourth oxygen is then more difficult to bind. The binding of oxygen to hemoglobin can be plotted as a function of the partial pressure of oxygen in the blood (x-axis) versus the relative Hb-oxygen saturation (y-axis). The resulting graph—an **oxygen dissociation curve**—is sigmoidal, or S-shaped ([link]). As the partial pressure of oxygen increases, the hemoglobin becomes increasingly saturated with oxygen.

Note:
Art Connection
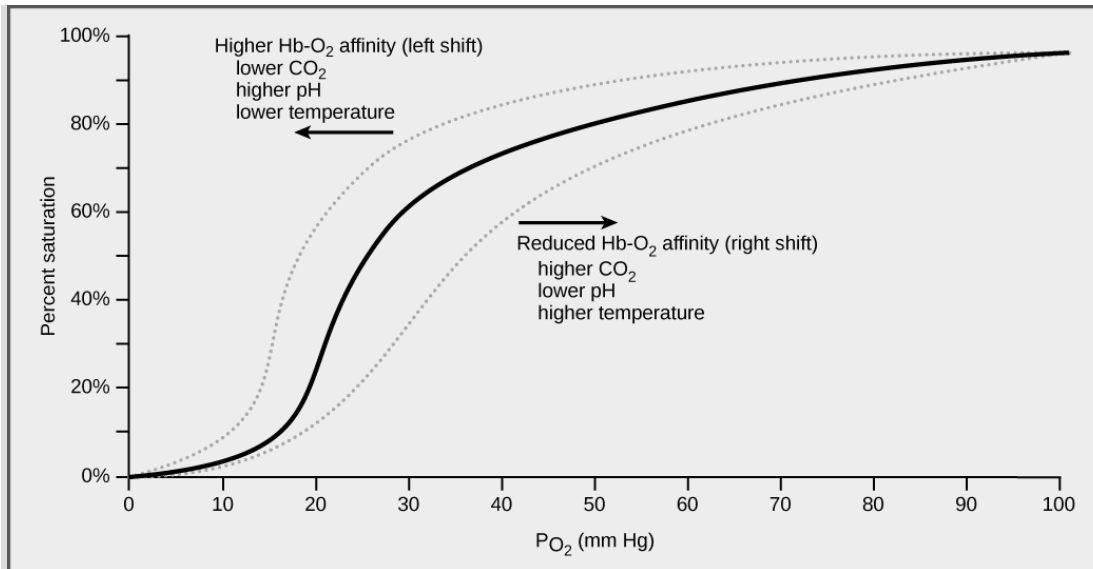
The oxygen dissociation curve demonstrates that, as the partial pressure of oxygen increases, more oxygen binds hemoglobin. However, the affinity of hemoglobin for oxygen may shift to the left or the right depending on environmental conditions.

The kidneys are responsible for removing excess H+ ions from the blood. If the kidneys fail, what would happen to blood pH and to hemoglobin affinity for oxygen?

Factors That Affect Oxygen Binding

The **oxygen-carrying capacity** of hemoglobin determines how much oxygen is carried in the blood. In addition to P_{O_2}, other environmental factors and diseases can affect oxygen carrying capacity and delivery.

Carbon dioxide levels, blood pH, and body temperature affect oxygen-carrying capacity ([link]). When carbon dioxide is in the blood, it reacts with water to form bicarbonate (HCO_3^-) and hydrogen ions (H$^+$). As the level of carbon dioxide in the blood increases, more H$^+$ is produced and the pH decreases. This increase in carbon dioxide and subsequent decrease in pH reduce the affinity of hemoglobin for oxygen. The oxygen dissociates

from the Hb molecule, shifting the oxygen dissociation curve to the right. Therefore, more oxygen is needed to reach the same hemoglobin saturation level as when the pH was higher. A similar shift in the curve also results from an increase in body temperature. Increased temperature, such as from increased activity of skeletal muscle, causes the affinity of hemoglobin for oxygen to be reduced.

Diseases like sickle cell anemia and thalassemia decrease the blood's ability to deliver oxygen to tissues and its oxygen-carrying capacity. In **sickle cell anemia**, the shape of the red blood cell is crescent-shaped, elongated, and stiffened, reducing its ability to deliver oxygen ([link]). In this form, red blood cells cannot pass through the capillaries. This is painful when it occurs. **Thalassemia** is a rare genetic disease caused by a defect in either the alpha or the beta subunit of Hb. Patients with thalassemia produce a high number of red blood cells, but these cells have lower-than-normal levels of hemoglobin. Therefore, the oxygen-carrying capacity is diminished.
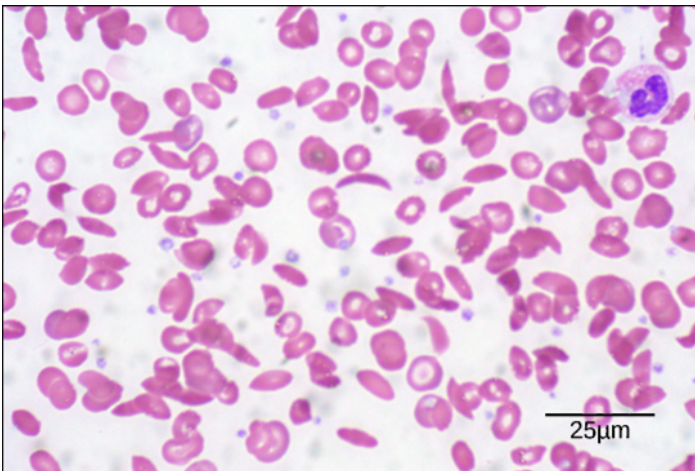
Individuals with sickle cell anemia have crescent-shaped red blood cells. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Transport of Carbon Dioxide in the Blood

Carbon dioxide molecules are transported in the blood from body tissues to the lungs by one of three methods: dissolution directly into the blood, binding to hemoglobin, or carried as a bicarbonate ion. Several properties of carbon dioxide in the blood affect its transport. First, carbon dioxide is more soluble in blood than oxygen. About 5 to 7 percent of all carbon dioxide is dissolved in the plasma. Second, carbon dioxide can bind to plasma proteins or can enter red blood cells and bind to hemoglobin. This form transports about 10 percent of the carbon dioxide. When carbon dioxide binds to hemoglobin, a molecule called **carbaminohemoglobin** is formed. Binding of carbon dioxide to hemoglobin is reversible. Therefore, when it reaches the lungs, the carbon dioxide can freely dissociate from the hemoglobin and be expelled from the body.

Third, the majority of carbon dioxide molecules (85 percent) are carried as part of the **bicarbonate buffer system**. In this system, carbon dioxide diffuses into the red blood cells. **Carbonic anhydrase (CA)** within the red blood cells quickly converts the carbon dioxide into carbonic acid (H_2CO_3). Carbonic acid is an unstable intermediate molecule that immediately dissociates into **bicarbonate ions** (HCO_3^-) and hydrogen (H^+) ions. Since carbon dioxide is quickly converted into bicarbonate ions, this reaction allows for the continued uptake of carbon dioxide into the blood down its concentration gradient. It also results in the production of H^+ ions. If too much H^+ is produced, it can alter blood pH. However, hemoglobin binds to the free H^+ ions and thus limits shifts in pH. The newly synthesized bicarbonate ion is transported out of the red blood cell into the liquid component of the blood in exchange for a chloride ion (Cl^-); this is called the **chloride shift**. When the blood reaches the lungs, the bicarbonate ion is transported back into the red blood cell in exchange for the chloride ion. The H^+ ion dissociates from the hemoglobin and binds to the bicarbonate ion. This produces the carbonic acid intermediate, which is converted back into carbon dioxide through the enzymatic action of CA. The carbon dioxide produced is expelled through the lungs during exhalation.
Equation:

$$\text{CO}_2 + \text{H}_2\text{O} \quad \leftrightarrow \quad \underset{\text{(carbonic acid)}}{\text{H}_2\text{CO}_3} \quad \leftrightarrow \quad \underset{\text{(bicarbonate)}}{\text{HCO}_3 + \text{H}^+}$$
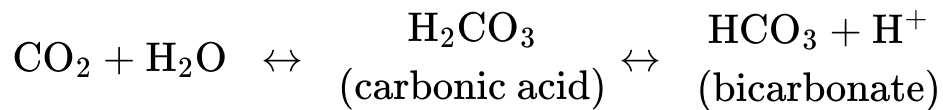
The benefit of the bicarbonate buffer system is that carbon dioxide is "soaked up" into the blood with little change to the pH of the system. This is important because it takes only a small change in the overall pH of the body for severe injury or death to result. The presence of this bicarbonate buffer system also allows for people to travel and live at high altitudes: When the partial pressure of oxygen and carbon dioxide change at high altitudes, the bicarbonate buffer system adjusts to regulate carbon dioxide while maintaining the correct pH in the body.

Carbon Monoxide Poisoning

While carbon dioxide can readily associate and dissociate from hemoglobin, other molecules such as carbon monoxide (CO) cannot. Carbon monoxide has a greater affinity for hemoglobin than oxygen. Therefore, when carbon monoxide is present, it binds to hemoglobin preferentially over oxygen. As a result, oxygen cannot bind to hemoglobin, so very little oxygen is transported through the body ([link]). Carbon monoxide is a colorless, odorless gas and is therefore difficult to detect. It is produced by gas-powered vehicles and tools. Carbon monoxide can cause headaches, confusion, and nausea; long-term exposure can cause brain damage or death. Administering 100 percent (pure) oxygen is the usual treatment for carbon monoxide poisoning. Administration of pure oxygen speeds up the separation of carbon monoxide from hemoglobin.
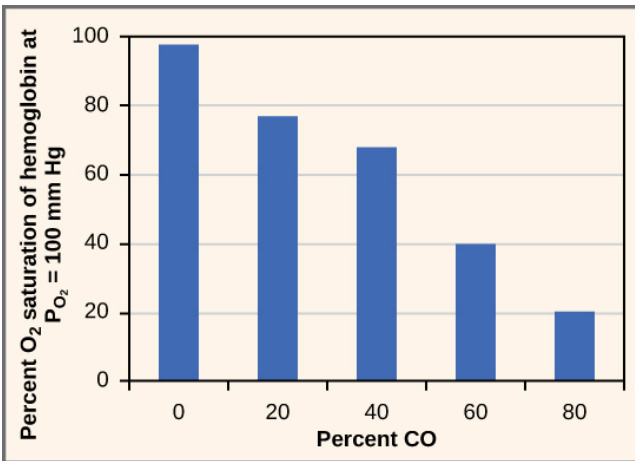
As percent CO increases, the oxygen saturation of hemoglobin decreases.

Section Summary

Hemoglobin is a protein found in red blood cells that is comprised of two alpha and two beta subunits that surround an iron-containing heme group. Oxygen readily binds this heme group. The ability of oxygen to bind increases as more oxygen molecules are bound to heme. Disease states and altered conditions in the body can affect the binding ability of oxygen, and increase or decrease its ability to dissociate from hemoglobin.

Carbon dioxide can be transported through the blood via three methods. It is dissolved directly in the blood, bound to plasma proteins or hemoglobin, or converted into bicarbonate. The majority of carbon dioxide is transported as part of the bicarbonate system. Carbon dioxide diffuses into red blood cells. Inside, carbonic anhydrase converts carbon dioxide into carbonic acid (H_2CO_3), which is subsequently hydrolyzed into bicarbonate (HCO_3^-) and H^+. The H^+ ion binds to hemoglobin in red blood cells, and bicarbonate is transported out of the red blood cells in exchange for a chloride ion. This is called the chloride shift. Bicarbonate leaves the red blood cells and enters the blood plasma. In the lungs, bicarbonate is transported back into the red

blood cells in exchange for chloride. The H^+ dissociates from hemoglobin and combines with bicarbonate to form carbonic acid with the help of carbonic anhydrase, which further catalyzes the reaction to convert carbonic acid back into carbon dioxide and water. The carbon dioxide is then expelled from the lungs.

Art Connections

Exercise:

Problem:

[link] The kidneys are responsible for removing excess H+ ions from the blood. If the kidneys fail, what would happen to blood pH and to hemoglobin affinity for oxygen?

Solution:

[link] The blood pH will drop and hemoglobin affinity for oxygen will decrease.

Review Questions

Exercise:

Problem:

Which of the following will NOT facilitate the transfer of oxygen to tissues?

    a. decreased body temperature
    b. decreased pH of the blood
    c. increased carbon dioxide
    d. increased exercise

Solution:

A

Exercise:

Problem:

The majority of carbon dioxide in the blood is transported by _____.

    a. binding to hemoglobin
    b. dissolution in the blood
    c. conversion to bicarbonate
    d. binding to plasma proteins

Solution:

C

Exercise:

Problem:

The majority of oxygen in the blood is transported by _____.

    a. dissolution in the blood
    b. being carried as bicarbonate ions
    c. binding to blood plasma
    d. binding to hemoglobin

Solution:

D

Free Response

Exercise:

Problem:

What would happen if no carbonic anhydrase were present in red blood cells?

Solution:

Without carbonic anhydrase, carbon dioxide would not be hydrolyzed into carbonic acid or bicarbonate. Therefore, very little carbon dioxide (only 15 percent) would be transported in the blood away from the tissues.

Exercise:

Problem:

How does the administration of 100 percent oxygen save a patient from carbon monoxide poisoning? Why wouldn't giving carbon dioxide work?

Solution:

Carbon monoxide has a higher affinity for hemoglobin than oxygen. This means that carbon monoxide will preferentially bind to hemoglobin over oxygen. Administration of 100 percent oxygen is an effective therapy because at that concentration, oxygen will displace the carbon monoxide from the hemoglobin.

Glossary

bicarbonate buffer system
　　system in the blood that absorbs carbon dioxide and regulates pH
　　levels

bicarbonate (HCO_3^-) ion
　　ion created when carbonic acid dissociates into H^+ and (HCO_3^-)

carbaminohemoglobin
      molecule that forms when carbon dioxide binds to hemoglobin

carbonic anhydrase (CA)
      enzyme that catalyzes carbon dioxide and water into carbonic acid

chloride shift
      chloride shift exchange of chloride for bicarbonate into or out of the
      red blood cell

heme group
      centralized iron-containing group that is surrounded by the alpha and
      beta subunits of hemoglobin

hemoglobin
      molecule in red blood cells that can bind oxygen, carbon dioxide, and
      carbon monoxide

oxygen-carrying capacity
      amount of oxygen that can be transported in the blood

oxygen dissociation curve
      curve depicting the affinity of oxygen for hemoglobin

sickle cell anemia
      genetic disorder that affects the shape of red blood cells, and their
      ability to transport oxygen and move through capillaries

thalassemia
      rare genetic disorder that results in mutation of the alpha or beta
      subunits of hemoglobin, creating smaller red blood cells with less
      hemoglobin

Introduction
class="introduction"

An athlete's nervous system is hard at work during the planning and execution of a movement as precise as a high jump. Parts of the nervous system are involved in determining how hard to push off and when to turn, as well as controlling the muscles throughout the body that make this complicated movement possible without knocking the bar down—all

in just a few seconds. (credit: modification of work by Shane T. McCoy, U.S. Navy)

When you're reading this book, your nervous system is performing several functions simultaneously. The visual system is processing what is seen on the page; the motor system controls the turn of the pages (or click of the mouse); the prefrontal cortex maintains attention. Even fundamental functions, like breathing and regulation of body temperature, are controlled by the nervous system. A nervous system is an organism's control center: it processes sensory information from outside (and inside) the body and controls all behaviors—from eating to sleeping to finding a mate.

Neurons and Glial Cells
By the end of this section, you will be able to:

- List and describe the functions of the structural components of a neuron
- List and describe the four main types of neurons
- Compare the functions of different types of glial cells

Nervous systems throughout the animal kingdom vary in structure and complexity, as illustrated by the variety of animals shown in [link]. Some organisms, like sea sponges, lack a true nervous system. Others, like jellyfish, lack a true brain and instead have a system of separate but connected nerve cells (neurons) called a "nerve net." Echinoderms such as sea stars have nerve cells that are bundled into fibers called nerves. Flatworms of the phylum Platyhelminthes have both a central nervous system (CNS), made up of a small "brain" and two nerve cords, and a peripheral nervous system (PNS) containing a system of nerves that extend throughout the body. The insect nervous system is more complex but also fairly decentralized. It contains a brain, ventral nerve cord, and ganglia (clusters of connected neurons). These ganglia can control movements and behaviors without input from the brain. Octopi may have the most complicated of invertebrate nervous systems—they have neurons that are organized in specialized lobes and eyes that are structurally similar to vertebrate species.
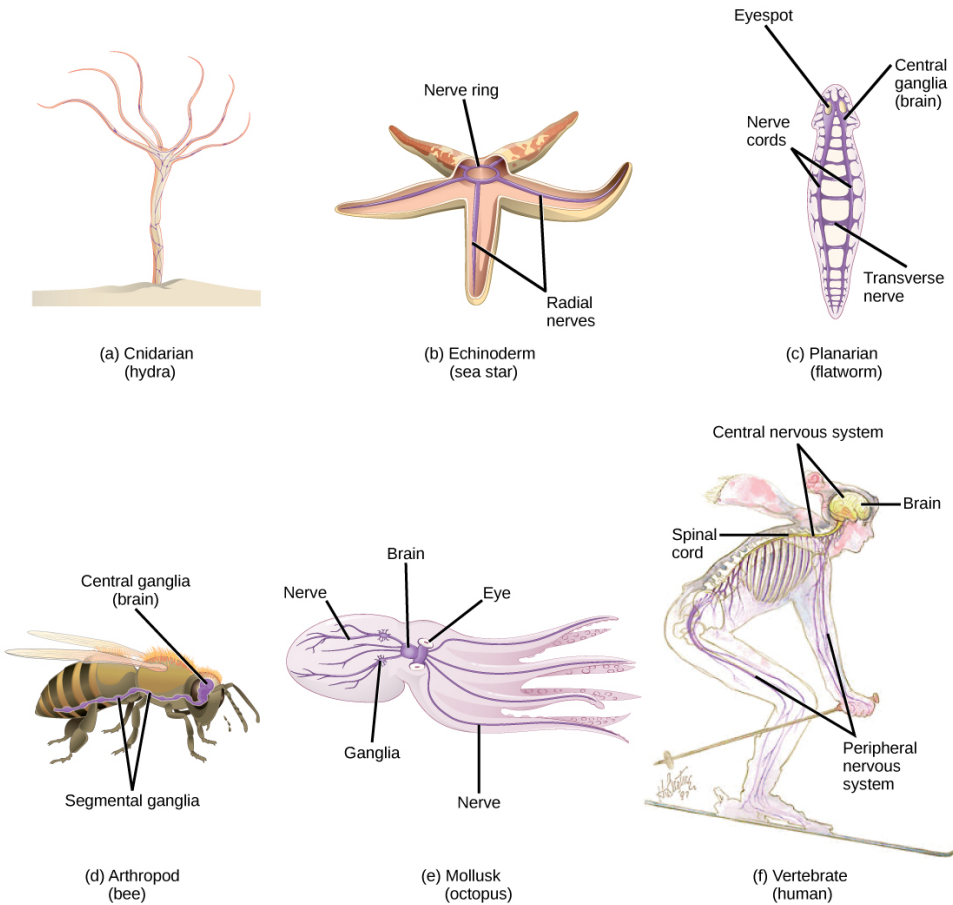
Nervous systems vary in structure and complexity. In (a) cnidarians, nerve cells form a decentralized nerve net. In (b) echinoderms, nerve cells are bundled into fibers called nerves. In animals exhibiting bilateral symmetry such as (c) planarians, neurons cluster into an anterior brain that processes information. In addition to a brain, (d) arthropods have clusters of nerve cell bodies, called peripheral ganglia, located along the ventral nerve cord. Mollusks such as squid and (e) octopi, which must hunt to survive, have complex brains containing millions of neurons. In (f) vertebrates, the brain and spinal cord comprise the central nervous system, while neurons extending into the rest of the body comprise the peripheral nervous system. (credit e: modification of work by Michael

Vecchione, Clyde F.E. Roper, and Michael J. Sweeney,
NOAA; credit f: modification of work by NIH)

Compared to invertebrates, vertebrate nervous systems are more complex, centralized, and specialized. While there is great diversity among different vertebrate nervous systems, they all share a basic structure: a CNS that contains a brain and spinal cord and a PNS made up of peripheral sensory and motor nerves. One interesting difference between the nervous systems of invertebrates and vertebrates is that the nerve cords of many invertebrates are located ventrally whereas the vertebrate spinal cords are located dorsally. There is debate among evolutionary biologists as to whether these different nervous system plans evolved separately or whether the invertebrate body plan arrangement somehow "flipped" during the evolution of vertebrates.

Note:
Link to Learning

Watch this video of biologist Mark Kirschner discussing the "flipping" phenomenon of vertebrate evolution.
https://www.openstaxcollege.org/l/vertebrate_evol

The nervous system is made up of **neurons**, specialized cells that can receive and transmit chemical or electrical signals, and **glia**, cells that provide support functions for the neurons by playing an information processing role that is complementary to neurons. A neuron can be compared to an electrical wire—it transmits a signal from one place to

another. Glia can be compared to the workers at the electric company who make sure wires go to the right places, maintain the wires, and take down wires that are broken. Although glia have been compared to workers, recent evidence suggests that also usurp some of the signaling functions of neurons.

There is great diversity in the types of neurons and glia that are present in different parts of the nervous system. There are four major types of neurons, and they share several important cellular components.

Neurons

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors—from basic reflexes to more complicated behaviors like finding food and courting mates. The ability of neurons to communicate with each other as well as with other types of cells underlies all of these behaviors.

Most neurons share the same cellular components. But neurons are also highly specialized—different types of neurons have different sizes and shapes that relate to their functional roles.

Parts of a Neuron

Like other cells, each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components. Neurons also contain unique structures, illustrated in [link] for receiving and sending the electrical signals that make neuronal communication possible. **Dendrites** are tree-like structures that extend away from the cell body to receive messages from other neurons at specialized junctions called **synapses**. Although some neurons do not have any dendrites, some types of neurons have multiple

dendrites. Dendrites can have small protrusions called dendritic spines, which further increase surface area for possible synaptic connections.

Once a signal is received by the dendrite, it then travels passively to the cell body. The cell body contains a specialized structure, the **axon hillock** that integrates signals from multiple synapses and serves as a junction between the cell body and an **axon**. An axon is a tube-like structure that propagates the integrated signal to specialized endings called **axon terminals**. These terminals in turn synapse on other neurons, muscle, or target organs. Chemicals released at axon terminals allow signals to be communicated to these other cells. Neurons usually have one or two axons, but some neurons, like amacrine cells in the retina, do not contain any axons. Some axons are covered with **myelin**, which acts as an insulator to minimize dissipation of the electrical signal as it travels down the axon, greatly increasing the speed on conduction. This insulation is important as the axon from a human motor neuron can be as long as a meter—from the base of the spine to the toes. The myelin sheath is not actually part of the neuron. Myelin is produced by glial cells. Along the axon there are periodic gaps in the myelin sheath. These gaps are called **nodes of Ranvier** and are sites where the signal is "recharged" as it travels along the axon.

It is important to note that a single neuron does not act alone—neuronal communication depends on the connections that neurons make with one another (as well as with other cells, like muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

Note:
Art Connection
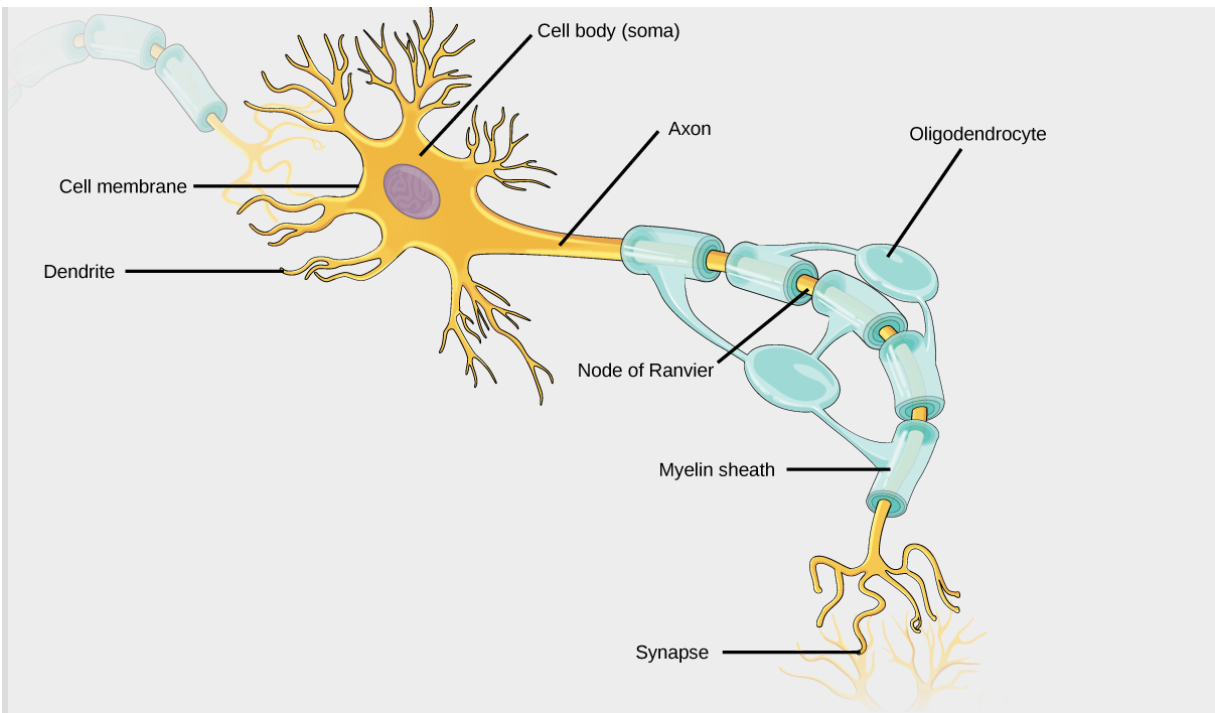
Neurons contain organelles common to many other cells, such as a nucleus and mitochondria. They also have more specialized structures, including dendrites and axons.

Which of the following statements is false?

a. The soma is the cell body of a nerve cell.
b. Myelin sheath provides an insulating layer to the dendrites.
c. Axons carry the signal from the soma to the target.
d. Dendrites carry the signal to the soma.

Types of Neurons

There are different types of neurons, and the functional role of a given neuron is intimately dependent on its structure. There is an amazing diversity of neuron shapes and sizes found in different parts of the nervous system (and across species), as illustrated by the neurons shown in [link].
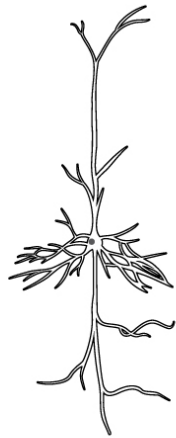
(a) Pyramidal cell of the
cerebral cortex
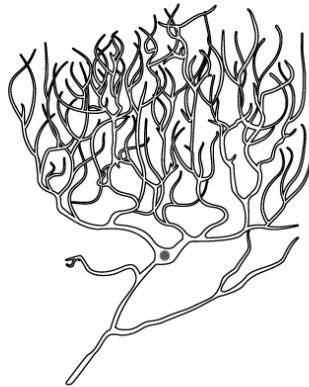
(b) Purkinje cell of the
cerebellar cortex
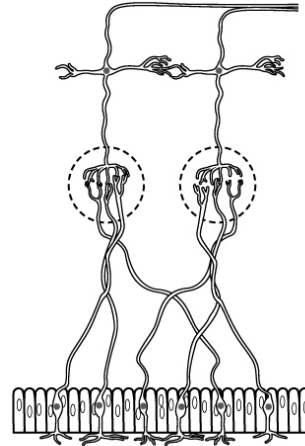
(c) Olfactory neurons

There is great diversity in the size and shape of neurons throughout the nervous system. Examples include (a) a pyramidal cell from the cerebral cortex, (b) a Purkinje cell from the cerebellar cortex, and (c) olfactory cells from the olfactory epithelium and olfactory bulb.

While there are many defined neuron cell subtypes, neurons are broadly divided into four basic types: unipolar, bipolar, multipolar, and pseudounipolar. [link] illustrates these four basic neuron types. Unipolar neurons have only one structure that extends away from the soma. These neurons are not found in vertebrates but are found in insects where they stimulate muscles or glands. A bipolar neuron has one axon and one dendrite extending from the soma. An example of a bipolar neuron is a retinal bipolar cell, which receives signals from photoreceptor cells that are sensitive to light and transmits these signals to ganglion cells that carry the signal to the brain. Multipolar neurons are the most common type of neuron. Each multipolar neuron contains one axon and multiple dendrites. Multipolar neurons can be found in the central nervous system (brain and spinal cord). An example of a multipolar neuron is a Purkinje cell in the cerebellum, which has many branching dendrites but only one axon. Pseudounipolar cells share characteristics with both unipolar and bipolar cells. A pseudounipolar cell has a single process that extends from the soma, like a unipolar cell, but this process later branches into two distinct

structures, like a bipolar cell. Most sensory neurons are pseudounipolar and have an axon that branches into two extensions: one connected to dendrites that receive sensory information and another that transmits this information to the spinal cord.
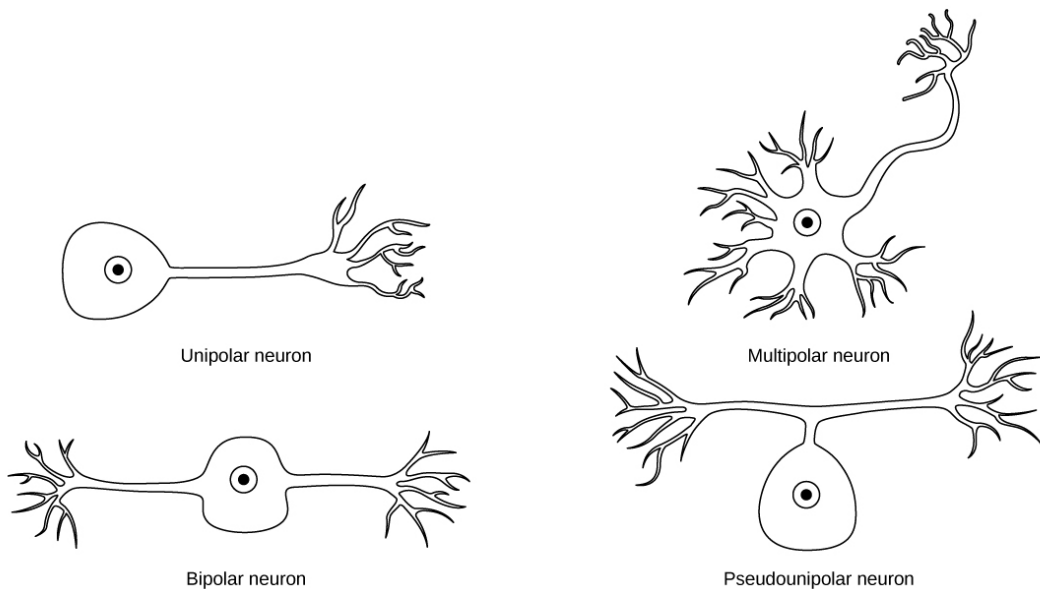
Neurons are broadly divided into four main types based on the number and placement of axons: (1) unipolar, (2) bipolar, (3) multipolar, and (4) pseudounipolar.

Note:
Everyday Connection
Neurogenesis
At one time, scientists believed that people were born with all the neurons they would ever have. Research performed during the last few decades indicates that neurogenesis, the birth of new neurons, continues into adulthood. Neurogenesis was first discovered in songbirds that produce new neurons while learning songs. For mammals, new neurons also play an important role in learning: about 1000 new neurons develop in the

hippocampus (a brain structure involved in learning and memory) each day. While most of the new neurons will die, researchers found that an increase in the number of surviving new neurons in the hippocampus correlated with how well rats learned a new task. Interestingly, both exercise and some antidepressant medications also promote neurogenesis in the hippocampus. Stress has the opposite effect. While neurogenesis is quite limited compared to regeneration in other tissues, research in this area may lead to new treatments for disorders such as Alzheimer's, stroke, and epilepsy.

How do scientists identify new neurons? A researcher can inject a compound called bromodeoxyuridine (BrdU) into the brain of an animal. While all cells will be exposed to BrdU, BrdU will only be incorporated into the DNA of newly generated cells that are in S phase. A technique called immunohistochemistry can be used to attach a fluorescent label to the incorporated BrdU, and a researcher can use fluorescent microscopy to visualize the presence of BrdU, and thus new neurons, in brain tissue. [link] is a micrograph which shows fluorescently labeled neurons in the hippocampus of a rat.
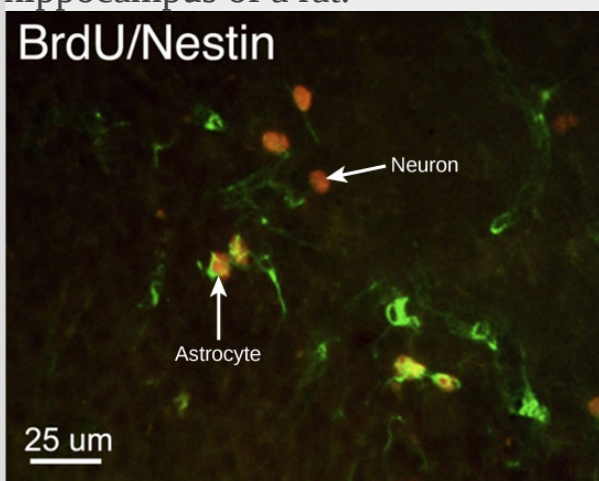
This micrograph shows fluorescently labeled new neurons in a rat hippocampus. Cells that are actively dividing have bromodoxyuridine (BrdU) incorporated into their DNA and are labeled in red. Cells that express glial fibrillary acidic

protein (GFAP) are labeled in green. Astrocytes, but not neurons, express GFAP. Thus, cells that are labeled both red and green are actively dividing astrocytes, whereas cells labeled red only are actively dividing neurons. (credit: modification of work by Dr. Maryam Faiz, et. al., University of Barcelona; scale-bar data from Matt Russell)

Glia

While glia are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of ten. Neurons would be unable to function without the

vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons, and provide myelin sheaths around axons. Scientists have recently discovered that they also play a role in responding to nerve activity and modulating communication between nerve cells. When glia do not function properly, the result can be disastrous—most brain tumors are caused by mutations in glia.

Types of Glia

There are several different types of glia with different functions, two of which are shown in [link]. **Astrocytes**, shown in [link]**a** make contact with both capillaries and neurons in the CNS. They provide nutrients and other substances to neurons, regulate the concentrations of ions and chemicals in the extracellular fluid, and provide structural support for synapses. Astrocytes also form the blood-brain barrier—a structure that blocks entrance of toxic substances into the brain. Astrocytes, in particular, have been shown through calcium imaging experiments to become active in response to nerve activity, transmit calcium waves between astrocytes, and modulate the activity of surrounding synapses. **Satellite glia** provide nutrients and structural support for neurons in the PNS. **Microglia** scavenge and degrade dead cells and protect the brain from invading microorganisms. **Oligodendrocytes**, shown in [link]**b** form myelin sheaths around axons in the CNS. One axon can be myelinated by several oligodendrocytes, and one oligodendrocyte can provide myelin for multiple neurons. This is distinctive from the PNS where a single **Schwann cell** provides myelin for only one axon as the entire Schwann cell surrounds the axon. **Radial glia** serve as scaffolds for developing neurons as they migrate to their end destinations. **Ependymal** cells line fluid-filled ventricles of the brain and the central canal of the spinal cord. They are involved in the production of cerebrospinal fluid, which serves as a cushion for the brain, moves the fluid between the spinal cord and the brain, and is a component for the choroid plexus.
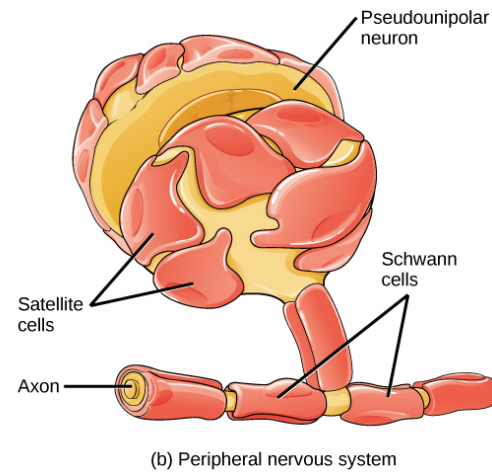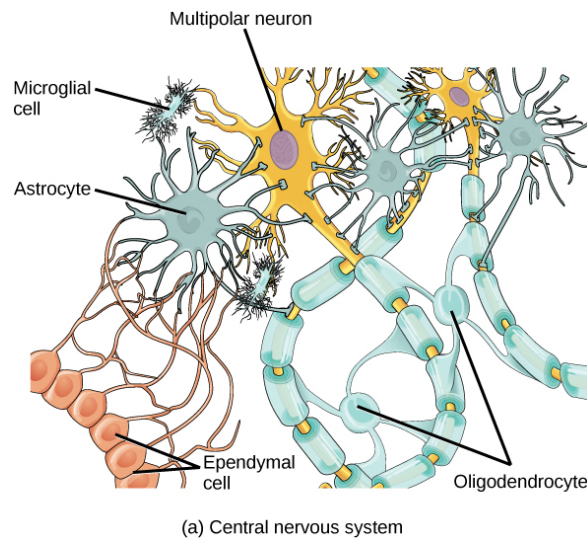
Glial cells support neurons and maintain their environment. Glial cells of the (a) central nervous system include oligodendrocytes, astrocytes, ependymal cells, and microglial cells. Oligodendrocytes form the myelin sheath around axons. Astrocytes provide nutrients to neurons, maintain their extracellular environment, and provide structural support. Microglia scavenge pathogens and dead cells. Ependymal cells produce cerebrospinal fluid that cushions the neurons. Glial cells of the (b) peripheral nervous system include Schwann cells, which form the myelin sheath, and satellite cells, which provide nutrients and structural support to neurons.
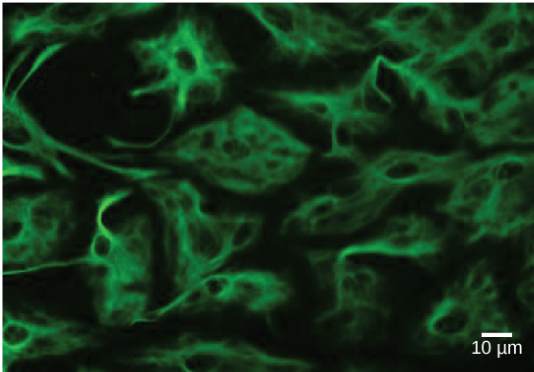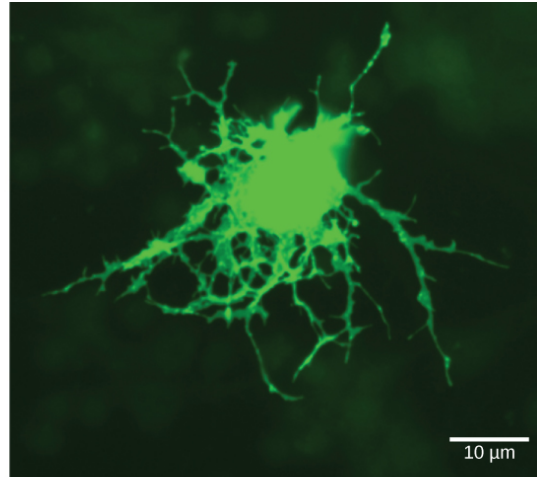
(a) Astrocyte   (b) Oligodendrocyte

(a) Astrocytes and (b) oligodendrocytes are glial cells of the central nervous system. (credit a: modification of work by Uniformed Services University; credit b: modification of work by Jurjen Broeke; scale-bar data from Matt Russell)

Section Summary

The nervous system is made up of neurons and glia. Neurons are specialized cells that are capable of sending electrical as well as chemical signals. Most neurons contain dendrites, which receive these signals, and axons that send signals to other neurons or tissues. There are four main types of neurons: unipolar, bipolar, multipolar, and pseudounipolar neurons. Glia are non-neuronal cells in the nervous system that support neuronal development and signaling. There are several types of glia that serve different functions.

Art Connections

Exercise:

**Problem:** [link] Which of the following statements is false?

a. The soma is the cell body of a nerve cell.
b. Myelin sheath provides an insulating layer to the dendrites.
c. Axons carry the signal from the soma to the target.
d. Dendrites carry the signal to the soma.

Solution:

[link] B

Review Questions

Exercise:

Problem:

Neurons contain _____, which can receive signals from other neurons.

a. axons
b. mitochondria
c. dendrites
d. Golgi bodies

Solution:

C

Exercise:

Problem:

A(n) _____ neuron has one axon and one dendrite extending directly from the cell body.

a. unipolar
b. bipolar
c. multipolar

d. pseudounipolar

Solution:

B

Exercise:

Problem:

Glia that provide myelin for neurons in the brain are called _____.

a. Schwann cells
b. oligodendrocytes
c. microglia
d. astrocytes

Solution:

B

Free Response

Exercise:

Problem:

How are neurons similar to other cells? How are they unique?

Solution:

Neurons contain organelles common to all cells, such as a nucleus and mitochondria. They are unique because they contain dendrites, which can receive signals from other neurons, and axons that can send these signals to other cells.

Exercise:

Problem:

Multiple sclerosis causes demyelination of axons in the brain and spinal cord. Why is this problematic?

Solution:

Myelin provides insulation for signals traveling along axons. Without myelin, signal transmission can slow down and degrade over time. This would slow down neuronal communication across the nervous system and affect all downstream functions.

Glossary

astrocyte
> glial cell in the central nervous system that provide nutrients, extracellular buffering, and structural support for neurons; also makes up the blood-brain barrier

axon
> tube-like structure that propagates a signal from a neuron's cell body to axon terminals

axon hillock
> electrically sensitive structure on the cell body of a neuron that integrates signals from multiple neuronal connections

axon terminal
> structure on the end of an axon that can form a synapse with another neuron

dendrite
> structure that extends away from the cell body to receive messages from other neurons

ependymal

cell that lines fluid-filled ventricles of the brain and the central canal of the spinal cord; involved in production of cerebrospinal fluid

glia
(also, glial cells) cells that provide support functions for neurons

microglia
glia that scavenge and degrade dead cells and protect the brain from invading microorganisms

myelin
fatty substance produced by glia that insulates axons

neuron
specialized cell that can receive and transmit electrical and chemical signals

nodes of Ranvier
gaps in the myelin sheath where the signal is recharged

oligodendrocyte
glial cell that myelinates central nervous system neuron axons

radial glia
glia that serve as scaffolds for developing neurons as they migrate to their final destinations

satellite glia
glial cell that provides nutrients and structural support for neurons in the peripheral nervous system

Schwann cell
glial cell that creates myelin sheath around a peripheral nervous system neuron axon

synapse
junction between two neurons where neuronal signals are communicated

How Neurons Communicate
By the end of this section, you will be able to:

- Describe the basis of the resting membrane potential
- Explain the stages of an action potential and how action potentials are propagated
- Explain the similarities and differences between chemical and electrical synapses
- Describe long-term potentiation and long-term depression

All functions performed by the nervous system—from a simple motor reflex to more advanced functions like making a memory or a decision—require neurons to communicate with one another. While humans use words and body language to communicate, neurons use electrical and chemical signals. Just like a person in a committee, one neuron usually receives and synthesizes messages from multiple other neurons before "making the decision" to send the message on to other neurons.

Nerve Impulse Transmission within a Neuron

For the nervous system to function, neurons must be able to send and receive signals. These signals are possible because each neuron has a charged cellular membrane (a voltage difference between the inside and the outside), and the charge of this membrane can change in response to neurotransmitter molecules released from other neurons and environmental stimuli. To understand how neurons communicate, one must first understand the basis of the baseline or 'resting' membrane charge.

Neuronal Charged Membranes

The lipid bilayer membrane that surrounds a neuron is impermeable to charged molecules or ions. To enter or exit the neuron, ions must pass through special proteins called ion channels that span the membrane. Ion channels have different configurations: open, closed, and inactive, as illustrated in [link]. Some ion channels need to be activated in order to open and allow ions to pass into or out of the cell. These ion channels are

sensitive to the environment and can change their shape accordingly. Ion channels that change their structure in response to voltage changes are called voltage-gated ion channels. Voltage-gated ion channels regulate the relative concentrations of different ions inside and outside the cell. The difference in total charge between the inside and outside of the cell is called the **membrane potential**.

Voltage-gated Na⁺ Channels

Outside cell

Cytoplasm
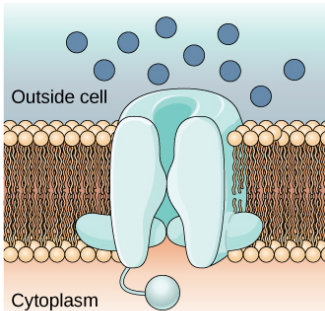
Closed At the resting potential, the channel is closed.
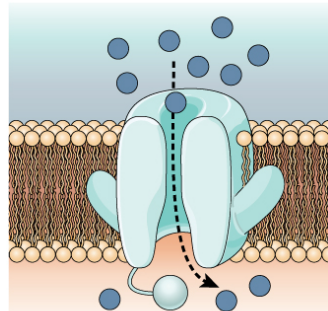
Open In response to a nerve impulse, the gate opens and Na⁺ enters the cell.
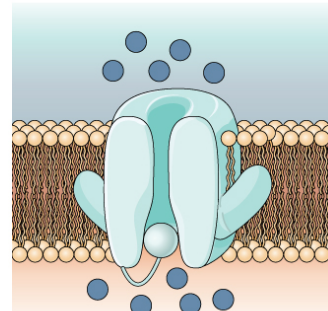
Inactivated For a brief period following activation, the channel does not open in response to a new signal.

Voltage-gated ion channels open in response to changes in membrane voltage. After activation, they become inactivated for a brief period and will no longer open in response to a signal.

Note:
Link to Learning

openstax COLLEGE™

Resting Membrane Potential

A neuron at rest is negatively charged: the inside of a cell is approximately 70 millivolts more negative than the outside (−70 mV, note that this number varies by neuron type and by species). This voltage is called the resting membrane potential; it is caused by differences in the concentrations of ions inside and outside the cell. If the membrane were equally permeable to all ions, each type of ion would flow across the membrane and the system would reach equilibrium. Because ions cannot simply cross the membrane at will, there are different concentrations of several ions inside and outside the cell, as shown in [link]. The difference in the number of positively charged potassium ions (K^+) inside and outside the cell dominates the resting membrane potential ([link]). When the membrane is at rest, K^+ ions accumulate inside the cell due to a net movement with the concentration gradient. The negative resting membrane potential is created and maintained by increasing the concentration of cations outside the cell (in the extracellular fluid) relative to inside the cell (in the cytoplasm). The negative charge within the cell is created by the cell membrane being more permeable to potassium ion movement than sodium ion movement. In neurons, potassium ions are maintained at high concentrations within the cell while sodium ions are maintained at high concentrations outside of the cell. The cell possesses potassium and sodium leakage channels that allow the two cations to diffuse down their concentration gradient. However, the neurons have far more potassium leakage channels than sodium leakage channels. Therefore, potassium diffuses out of the cell at a much faster rate than sodium leaks in. Because more cations are leaving the cell than are entering, this causes the interior of the cell to be negatively charged relative to the outside of the cell. The actions of the sodium potassium pump help to maintain the resting potential, once established. Recall that sodium potassium pumps brings two K^+ ions into the cell while removing three Na^+ ions per ATP consumed. As more cations are expelled from the cell than taken in, the inside of the cell remains negatively charged relative to the

extracellular fluid. It should be noted that chloride ions (Cl⁻) tend to accumulate outside of the cell because they are repelled by negatively-charged proteins within the cytoplasm.

Ion Concentration Inside and Outside Neurons			
Ion	**Extracellular concentration (mM)**	**Intracellular concentration (mM)**	**Ratio outside/inside**
Na^+	145	12	12
K+	4	155	0.026
Cl^-	120	4	30
Organic anions (A−)	—	100	

The resting membrane potential is a result of different concentrations inside and outside the cell.

0 mV

−80 mV   +40 mV

Extracellular fluid

Na⁺   Na⁺   Na⁺   Na⁺   Na⁺   Na⁺   Na⁺   Na⁺   Na⁺

Na⁺   Na⁺   Na⁺   K⁺ channel   Na⁺   K⁺   Na⁺   Na⁺ channel

Cystoplasm

K⁺   K⁺   K⁺   K⁺   K⁺   Na⁺   K⁺

K⁺   K⁺   K⁺   ATP   ADP   Na⁺   K⁺   K⁺
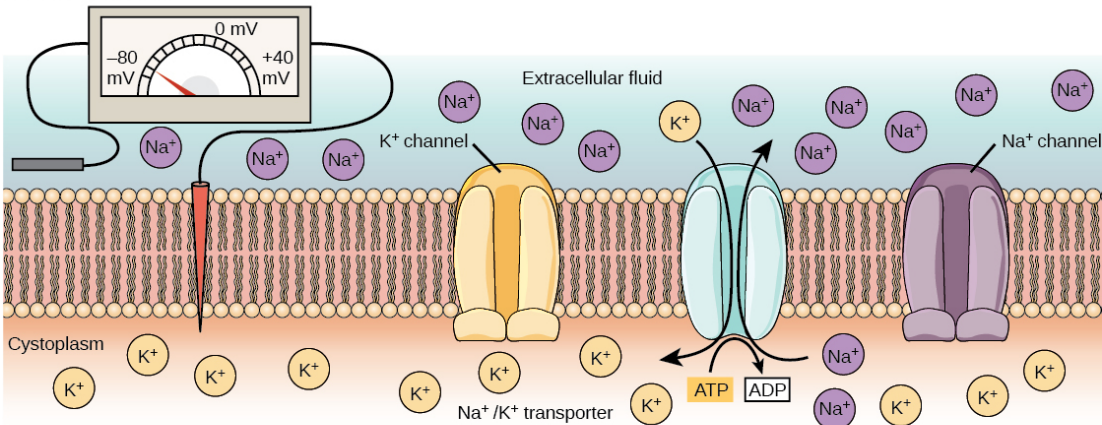
Na⁺/K⁺ transporter

At the resting potential, all voltage-gated Na⁺ channels and most voltage-gated K⁺ channels are closed. The Na⁺/K⁺ transporter pumps K⁺ ions into the cell and Na⁺ ions out.

(b) Depolarization

0 mV

−80 mV   +40 mV

Na⁺   Na⁺   Na⁺   Na⁺   Na⁺   Na⁺   Na⁺

Na⁺   Na⁺   K⁺ channel   Na⁺   K⁺   Na⁺   Na⁺ channel

Na⁺

K⁺   K⁺   K⁺   K⁺   K⁺   Na⁺

K⁺   K⁺   Na⁺   Na⁺   K⁺   K⁺

Na⁺/K⁺ transporter
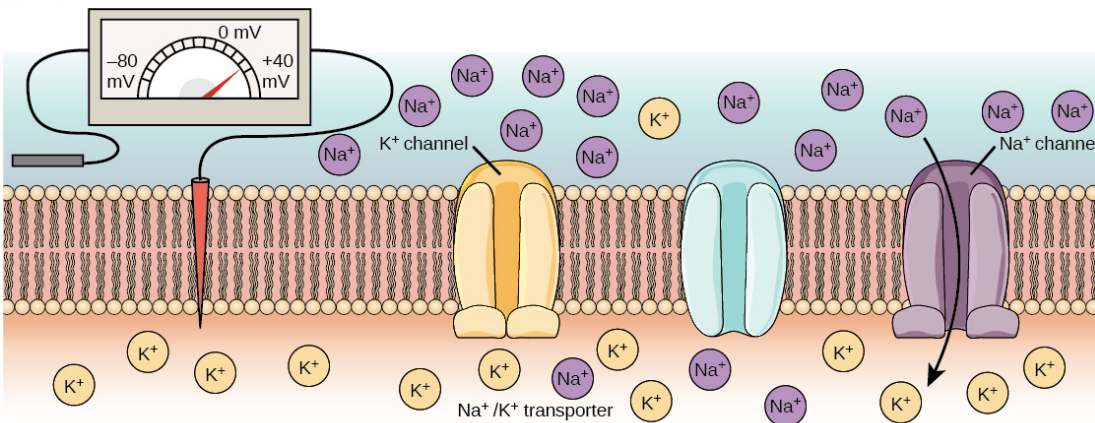
In response to a depolarization, some Na⁺ channels open, allowing Na⁺ ions to enter the cell. The membrane starts to depolarize (the charge across the membrane lessens). If the threshold of excitation is reached, all the Na⁺ channels open.

(c) Hyperpolarization

0 mV

−80 mV   +40 mV

Na⁺   K⁺   K⁺   K⁺

K⁺   K⁺   K⁺   K⁺ channel   K⁺   Na⁺   K⁺   Na⁺ channel

Na⁺   Na⁺

K⁺   Na⁺

Na⁺   Na⁺   Na⁺   K⁺   Na⁺   Na⁺   Na⁺

Na⁺   K⁺   Na⁺

Na⁺/K⁺ transporter
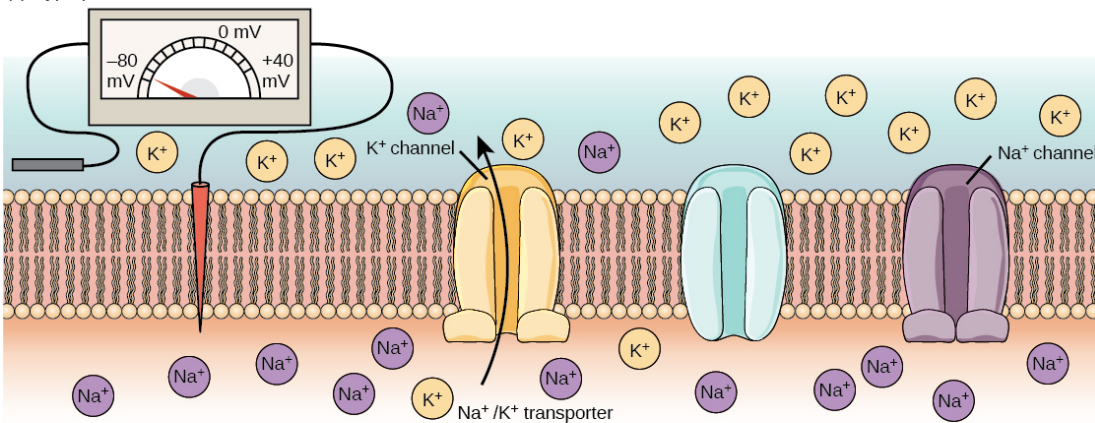
At the peak action potential, Na⁺ channels close while K⁺ channels open. K⁺ leaves the cell, and the membrane eventually becomes hyperpolarized.

The (a) resting membrane potential is a result of different concentrations of Na⁺ and K⁺ ions inside and outside the cell.

A nerve impulse causes Na$^+$ to enter the cell, resulting in (b) depolarization. At the peak action potential, K$^+$ channels open and the cell becomes (c) hyperpolarized.

Action Potential

A neuron can receive input from other neurons and, if this input is strong enough, send the signal to downstream neurons. Transmission of a signal between neurons is generally carried by a chemical called a neurotransmitter. Transmission of a signal within a neuron (from dendrite to axon terminal) is carried by a brief reversal of the resting membrane potential called an **action potential**. When neurotransmitter molecules bind to receptors located on a neuron's dendrites, ion channels open. At excitatory synapses, this opening allows positive ions to enter the neuron and results in **depolarization** of the membrane—a decrease in the difference in voltage between the inside and outside of the neuron. A stimulus from a sensory cell or another neuron depolarizes the target neuron to its threshold potential (-55 mV). Na$^+$ channels in the axon hillock open, allowing positive ions to enter the cell ([link] and [link]). Once the sodium channels open, the neuron completely depolarizes to a membrane potential of about +40 mV. Action potentials are considered an "all-or nothing" event, in that, once the threshold potential is reached, the neuron always completely depolarizes. Once depolarization is complete, the cell must now "reset" its membrane voltage back to the resting potential. To accomplish this, the Na$^+$ channels close and cannot be opened. This begins the neuron's **refractory period**, in which it cannot produce another action potential because its sodium channels will not open. At the same time, voltage-gated K$^+$ channels open, allowing K$^+$ to leave the cell. As K$^+$ ions leave the cell, the membrane potential once again becomes negative. The diffusion of K$^+$ out of the cell actually **hyperpolarizes** the cell, in that the membrane potential becomes more negative than the cell's normal resting potential. At this point, the sodium channels will return to their resting state, meaning they are ready to open again if the membrane potential again exceeds the

threshold potential. Eventually the extra K^+ ions diffuse out of the cell through the potassium leakage channels, bringing the cell from its hyperpolarized state, back to its resting membrane potential.

Note:
Art Connection
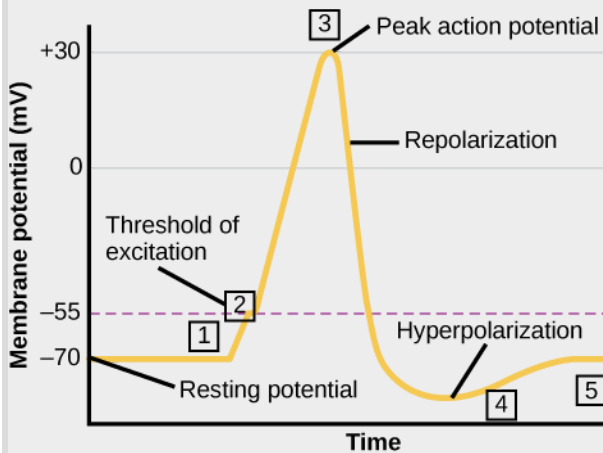
The formation of an action potential can be divided into five steps: (1) A stimulus from a sensory cell or another neuron causes the target cell to depolarize toward the threshold potential. (2) If the threshold of excitation is reached, all Na^+ channels open and the membrane depolarizes. (3) At the peak action potential, K^+ channels open and K^+ begins to leave the cell. At the same time, Na^+ channels close. (4) The membrane becomes hyperpolarized as K^+ ions continue to leave the cell. The hyperpolarized membrane is in

a refractory period and cannot fire. (5) The K^+ channels close and the Na^+/K^+ transporter restores the resting potential.

Potassium channel blockers, such as amiodarone and procainamide, which are used to treat abnormal electrical activity in the heart, called cardiac dysrhythmia, impede the movement of K^+ through voltage-gated K^+ channels. Which part of the action potential would you expect potassium channels to affect?

Soma   Axon   Axon terminal

Direction of travel of action potential

a. In response to a signal, the soma end of the axon becomes depolarized.

Depolarized

b. The depolarization spreads down the axon. Meanwhile, the first part of the membrane repolarizes. Because Na^+ channels are inactivated and additional K^+ channels have opened, the membrane cannot depolarize again.

Repolarizing   Depolarized   Resting

c. The action potential continues to travel down the axon.

Resting   Repolarizing   Depolarized
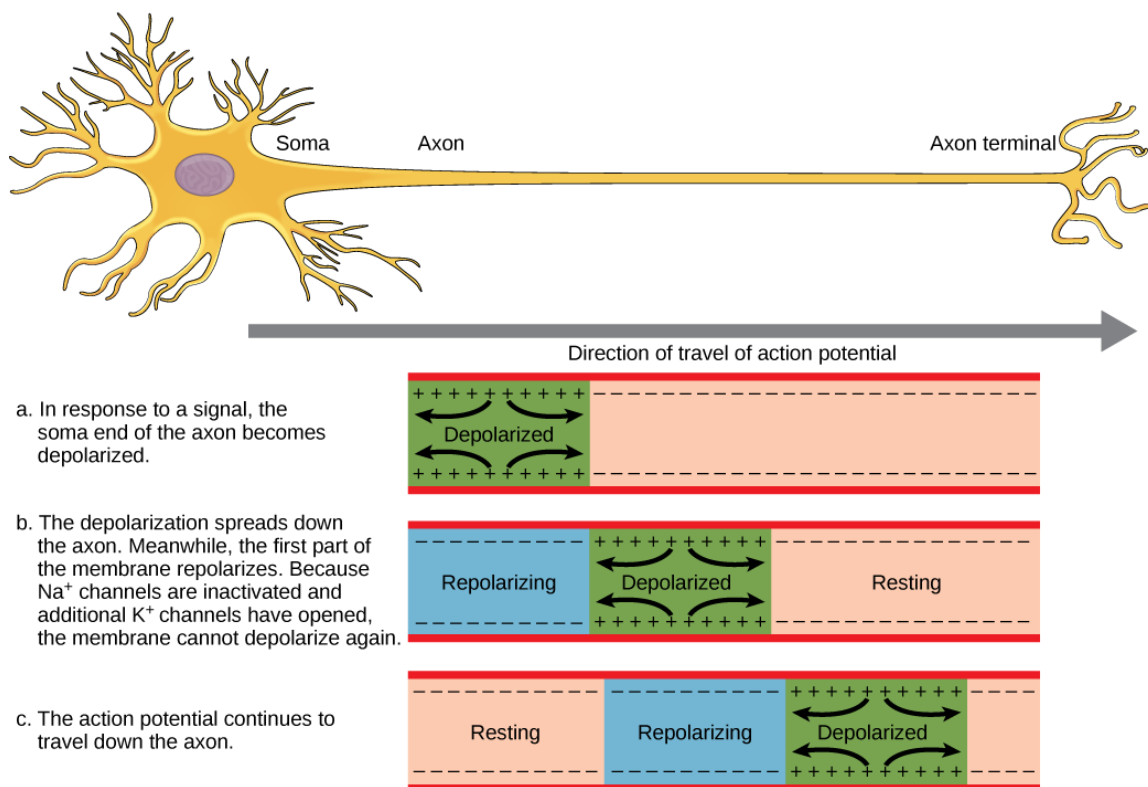
The action potential is conducted down the axon as the axon membrane depolarizes, then repolarizes.

Myelin and the Propagation of the Action Potential

For an action potential to communicate information to another neuron, it must travel along the axon and reach the axon terminals where it can initiate neurotransmitter release. The speed of conduction of an action potential along an axon is influenced by both the diameter of the axon and the axon's resistance to current leak. Myelin acts as an insulator that prevents current from leaving the axon; this increases the speed of action potential conduction. In demyelinating diseases like multiple sclerosis, action potential conduction slows because current leaks from previously insulated axon areas. The nodes of Ranvier, illustrated in [link] are gaps in the myelin sheath along the axon. These unmyelinated spaces are about one micrometer long and contain voltage gated Na^+ and K^+ channels. Flow of ions through these channels, particularly the Na^+ channels, regenerates the action potential over and over again along the axon. This 'jumping' of the action potential from one node to the next is called **saltatory conduction**. If nodes of Ranvier were not present along an axon, the action potential would propagate very slowly since Na^+ and K^+ channels would have to continuously regenerate action potentials at every point along the axon instead of at specific points. Nodes of Ranvier also save energy for the neuron since the channels only need to be present at the nodes and not along the entire axon.
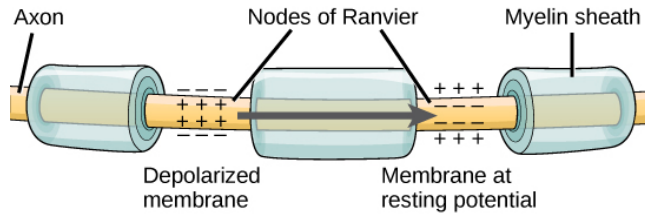
Nodes of Ranvier are gaps in
myelin coverage along axons.
Nodes contain voltage-gated K^+
and Na^+ channels. Action
potentials travel down the axon by
jumping from one node to the
next.

Synaptic Transmission

The synapse or "gap" is the place where information is transmitted from
one neuron to another. Synapses usually form between axon terminals and
dendritic spines, but this is not universally true. There are also axon-to-
axon, dendrite-to-dendrite, and axon-to-cell body synapses. The neuron
transmitting the signal is called the presynaptic neuron, and the neuron
receiving the signal is called the postsynaptic neuron. Note that these
designations are relative to a particular synapse—most neurons are both
presynaptic and postsynaptic. There are two types of synapses: chemical
and electrical.

Chemical Synapse

When an action potential reaches the axon terminal it depolarizes the
membrane and opens voltage-gated Na^+ channels. Na^+ ions enter the cell,
further depolarizing the presynaptic membrane. This depolarization causes
voltage-gated Ca^{2+} channels to open. Calcium ions entering the cell initiate
a signaling cascade that causes small membrane-bound vesicles, called

synaptic vesicles, containing neurotransmitter molecules to fuse with the presynaptic membrane. Synaptic vesicles are shown in [link], which is an image from a scanning electron microscope.
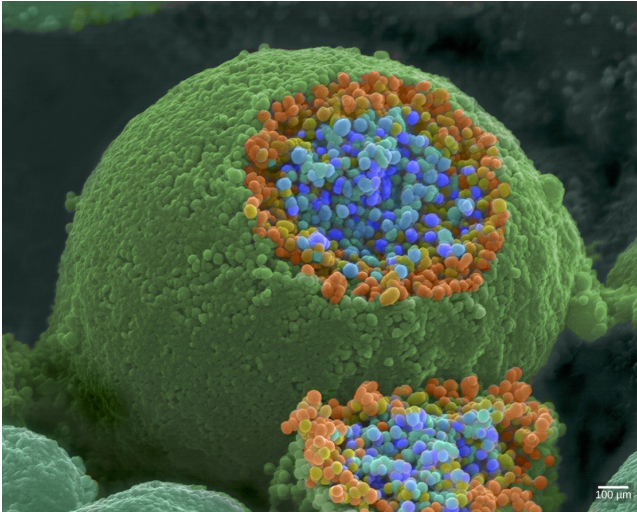
This pseudocolored image taken with a scanning electron microscope shows an axon terminal that was broken open to reveal synaptic vesicles (blue and orange) inside the neuron. (credit: modification of work by Tina Carvalho, NIH-NIGMS; scale-bar data from Matt Russell)

Fusion of a vesicle with the presynaptic membrane causes neurotransmitter to be released into the **synaptic cleft**, the extracellular space between the presynaptic and postsynaptic membranes, as illustrated in [link]. The neurotransmitter diffuses across the synaptic cleft and binds to receptor proteins on the postsynaptic membrane.

Presynaptic neuron

① Action potential arrives at axon terminal.

Axon terminal

③ Ca²⁺ entry causes neurotransmitter-containing synaptic vesicles to release their contents by exocytosis.

Synaptic vesicles

Synaptic cleft

② Voltage-gated Ca²⁺ channels open and Ca²⁺ enters the axon terminal.

Ca²⁺   Ca²⁺

④ Neurotransmitter diffuses across the synaptic cleft and binds to ligand-gated ion channels on the postsynaptic membrane.

Postsynaptic neuron

Localized membrane potential

Ion movement

Neurotransmitter   Graded potential

+ + + + + – – – – – –   – – – – – + + + + +

– – – – – + + + + +   + + + + + – – – – –

Open ligand-gated ion channel

Cytoplasm

⑤ Binding of neurotransmitter opens ligand-gated ion channels, resulting in graded potentials.

Presynaptic neuron

Diffusion away from synapse

Reuptake by presynaptic neuron

Enzymatic degradation

Postsynaptic neuron   Closed ligand-gated ion channel
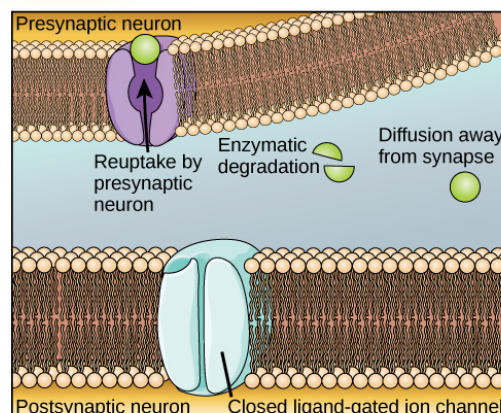
⑥ Reuptake by the presynapic neuron, enzymatic degradation, and diffusion reduce neurotransmitter levels, terminating the signal.

Communication at chemical synapses requires release of neurotransmitters. When the presynaptic membrane is depolarized, voltage-gated Ca²⁺ channels open and allow Ca²⁺ to enter the cell. The calcium entry causes synaptic vesicles to fuse

with the membrane and release neurotransmitter molecules into the synaptic cleft. The neurotransmitter diffuses across the synaptic cleft and binds to ligand-gated ion channels in the postsynaptic membrane, resulting in a localized depolarization or hyperpolarization of the postsynaptic neuron.

The binding of a specific neurotransmitter causes particular ion channels, in this case ligand-gated channels, on the postsynaptic membrane to open. Neurotransmitters can either have excitatory or inhibitory effects on the postsynaptic membrane, as detailed in [link]. For example, when acetylcholine is released at the synapse between a nerve and muscle (called the neuromuscular junction) by a presynaptic neuron, it causes postsynaptic Na^+ channels to open. Na^+ enters the postsynaptic cell and causes the postsynaptic membrane to depolarize. This depolarization is called an **excitatory postsynaptic potential (EPSP)** and makes the postsynaptic neuron more likely to fire an action potential. Release of neurotransmitter at inhibitory synapses causes **inhibitory postsynaptic potentials (IPSPs)**, a hyperpolarization of the presynaptic membrane. For example, when the neurotransmitter GABA (gamma-aminobutyric acid) is released from a presynaptic neuron, it binds to and opens Cl^- channels. Cl^- ions enter the cell and hyperpolarizes the membrane, making the neuron less likely to fire an action potential.

Once neurotransmission has occurred, the neurotransmitter must be removed from the synaptic cleft so the postsynaptic membrane can "reset" and be ready to receive another signal. This can be accomplished in three ways: the neurotransmitter can diffuse away from the synaptic cleft, it can be degraded by enzymes in the synaptic cleft, or it can be recycled (sometimes called reuptake) by the presynaptic neuron. Several drugs act at this step of neurotransmission. For example, some drugs that are given to Alzheimer's patients work by inhibiting acetylcholinesterase, the enzyme that degrades acetylcholine. This inhibition of the enzyme essentially increases neurotransmission at synapses that release acetylcholine. Once released, the acetylcholine stays in the cleft and can continually bind and unbind to postsynaptic receptors.

Neurotransmitter Function and Location		
Neurotransmitter	**Example**	**Location**
Acetylcholine	—	CNS and/or PNS
Biogenic amine	Dopamine, serotonin, norepinephrine	CNS and/or PNS
Amino acid	Glycine, glutamate, aspartate, gamma aminobutyric acid	CNS
Neuropeptide	Substance P, endorphins	CNS and/or PNS

Electrical Synapse

While electrical synapses are fewer in number than chemical synapses, they are found in all nervous systems and play important and unique roles. The mode of neurotransmission in electrical synapses is quite different from that in chemical synapses. In an electrical synapse, the presynaptic and postsynaptic membranes are very close together and are actually physically connected by channel proteins forming gap junctions. Gap junctions allow current to pass directly from one cell to the next. In addition to the ions that carry this current, other molecules, such as ATP, can diffuse through the large gap junction pores.

There are key differences between chemical and electrical synapses. Because chemical synapses depend on the release of neurotransmitter molecules from synaptic vesicles to pass on their signal, there is an approximately one millisecond delay between when the axon potential

reaches the presynaptic terminal and when the neurotransmitter leads to opening of postsynaptic ion channels. Additionally, this signaling is unidirectional. Signaling in electrical synapses, in contrast, is virtually instantaneous (which is important for synapses involved in key reflexes), and some electrical synapses are bidirectional. Electrical synapses are also more reliable as they are less likely to be blocked, and they are important for synchronizing the electrical activity of a group of neurons. For example, electrical synapses in the thalamus are thought to regulate slow-wave sleep, and disruption of these synapses can cause seizures.

Signal Summation

Sometimes a single EPSP is strong enough to induce an action potential in the postsynaptic neuron, but often multiple presynaptic inputs must create EPSPs around the same time for the postsynaptic neuron to be sufficiently depolarized to fire an action potential. This process is called **summation** and occurs at the axon hillock, as illustrated in [link]. Additionally, one neuron often has inputs from many presynaptic neurons—some excitatory and some inhibitory—so IPSPs can cancel out EPSPs and vice versa. It is the net change in postsynaptic membrane voltage that determines whether the postsynaptic cell has reached its threshold of excitation needed to fire an action potential. Together, synaptic summation and the threshold for excitation act as a filter so that random "noise" in the system is not transmitted as important information.
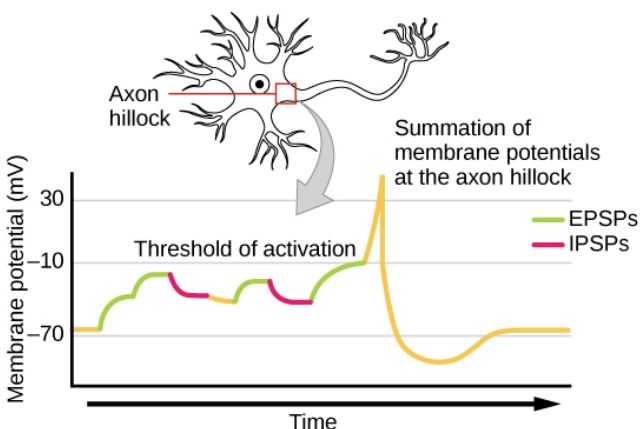
A single neuron can receive both excitatory and inhibitory inputs from multiple neurons, resulting in local membrane depolarization (EPSP input) and hyperpolarization (IPSP input). All these inputs are added together at the axon hillock. If the EPSPs are strong enough to overcome the IPSPs and reach the threshold of excitation, the neuron will fire.

Note:
Everyday Connection

Brain-computer interface

Amyotrophic lateral sclerosis (ALS, also called Lou Gehrig's Disease) is a neurological disease characterized by the degeneration of the motor neurons that control voluntary movements. The disease begins with muscle weakening and lack of coordination and eventually destroys the neurons that control speech, breathing, and swallowing; in the end, the disease can lead to paralysis. At that point, patients require assistance from machines to be able to breathe and to communicate. Several special technologies have been developed to allow "locked-in" patients to communicate with the rest of the world. One technology, for example, allows patients to type out sentences by twitching their cheek. These sentences can then be read aloud by a computer.

A relatively new line of research for helping paralyzed patients, including those with ALS, to communicate and retain a degree of self-sufficiency is called brain-computer interface (BCI) technology and is illustrated in [link]. This technology sounds like something out of science fiction: it allows paralyzed patients to control a computer using only their thoughts. There are several forms of BCI. Some forms use EEG recordings from electrodes taped onto the skull. These recordings contain information from

large populations of neurons that can be decoded by a computer. Other forms of BCI require the implantation of an array of electrodes smaller than a postage stamp in the arm and hand area of the motor cortex. This form of BCI, while more invasive, is very powerful as each electrode can record actual action potentials from one or more neurons. These signals are then sent to a computer, which has been trained to decode the signal and feed it to a tool—such as a cursor on a computer screen. This means that a patient with ALS can use e-mail, read the Internet, and communicate with others by thinking of moving his or her hand or arm (even though the paralyzed patient cannot make that bodily movement). Recent advances have allowed a paralyzed locked-in patient who suffered a stroke 15 years ago to control a robotic arm and even to feed herself coffee using BCI technology.

Despite the amazing advancements in BCI technology, it also has limitations. The technology can require many hours of training and long periods of intense concentration for the patient; it can also require brain surgery to implant the devices.
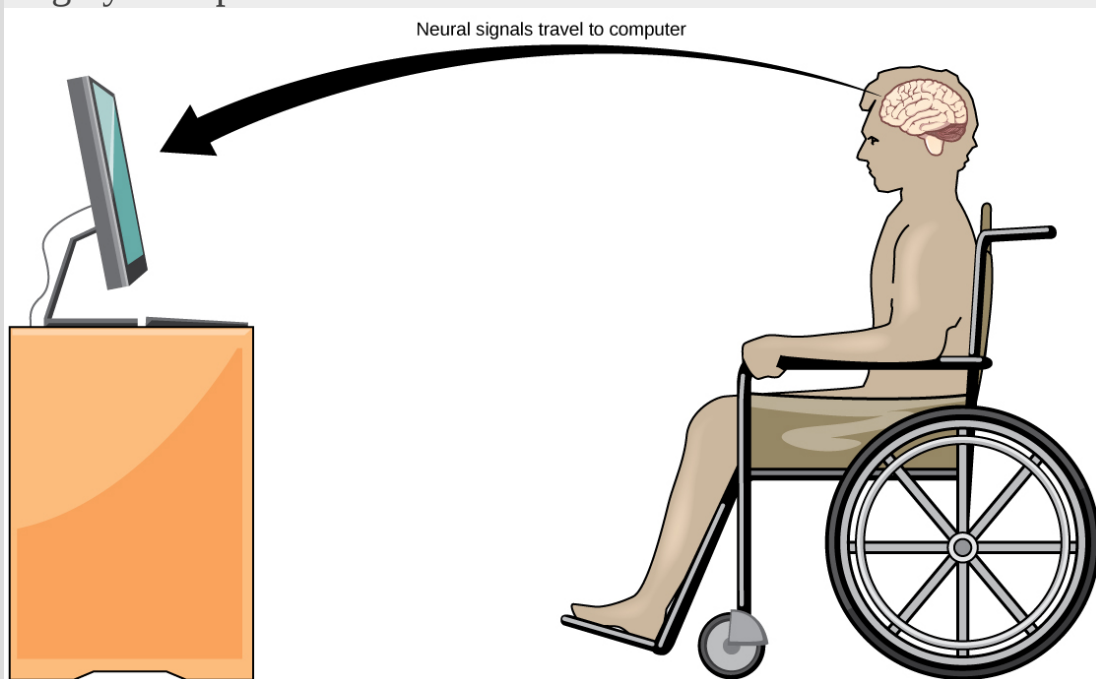
With brain-computer interface technology, neural signals from a paralyzed patient are collected, decoded, and then fed to a tool, such as a computer, a wheelchair, or a robotic arm.

Synaptic Plasticity

Synapses are not static structures. They can be weakened or strengthened. They can be broken, and new synapses can be made. Synaptic plasticity allows for these changes, which are all needed for a functioning nervous system. In fact, synaptic plasticity is the basis of learning and memory. Two processes in particular, long-term potentiation (LTP) and long-term depression (LTD) are important forms of synaptic plasticity that occur in synapses in the hippocampus, a brain region that is involved in storing memories.

Long-term Potentiation (LTP)

Long-term potentiation (LTP) is a persistent strengthening of a synaptic connection. LTP is based on the Hebbian principle: cells that fire together wire together. There are various mechanisms, none fully understood, behind the synaptic strengthening seen with LTP. One known mechanism involves

a type of postsynaptic glutamate receptor, called NMDA (N-Methyl-D-aspartate) receptors, shown in [link]. These receptors are normally blocked by magnesium ions; however, when the postsynaptic neuron is depolarized by multiple presynaptic inputs in quick succession (either from one neuron or multiple neurons), the magnesium ions are forced out allowing Ca ions to pass into the postsynaptic cell. Next, Ca^{2+} ions entering the cell initiate a signaling cascade that causes a different type of glutamate receptor, called AMPA (α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid) receptors, to be inserted into the postsynaptic membrane, since activated AMPA receptors allow positive ions to enter the cell. So, the next time glutamate is released from the presynaptic membrane, it will have a larger excitatory effect (EPSP) on the postsynaptic cell because the binding of glutamate to these AMPA receptors will allow more positive ions into the cell. The insertion of additional AMPA receptors strengthens the synapse and means that the postsynaptic neuron is more likely to fire in response to presynaptic neurotransmitter release. Some drugs of abuse co-opt the LTP pathway, and this synaptic strengthening can lead to addiction.

Long-term Depression (LTD)

Long-term depression (LTD) is essentially the reverse of LTP: it is a long-term weakening of a synaptic connection. One mechanism known to cause LTD also involves AMPA receptors. In this situation, calcium that enters through NMDA receptors initiates a different signaling cascade, which results in the removal of AMPA receptors from the postsynaptic membrane, as illustrated in [link]. The decrease in AMPA receptors in the membrane makes the postsynaptic neuron less responsive to glutamate released from the presynaptic neuron. While it may seem counterintuitive, LTD may be just as important for learning and memory as LTP. The weakening and pruning of unused synapses allows for unimportant connections to be lost and makes the synapses that have undergone LTP that much stronger by comparison.

Presynaptic terminal

Glutamate

LTP

Mg²⁺

NMDA receptor

Ca²⁺

Postsynaptic terminal

The NMDA receptor is activated by glutamate binding, but only after depolarization removes inhibitory Mg²⁺. Once the Mg²⁺ is removed, Ca²⁺ can enter the cell.

Presynaptic terminal

Glu

LTD

AMPA receptor

Ca²⁺

Postsynaptic terminal

Some AMPA receptors are present in the membrane initially. In response to an increase in intracellular Ca2⁺, more are inserted.

Presynaptic terminal

Glu

Ca²⁺

Postsynaptic terminal

Low-frequency stimulation results in a different Ca²⁺-signaling cascade. AMPA receptor is removed from the membrane, and as a result, the nerve cell becomes less responsive to glutamate.

Calcium entry through postsynaptic NMDA receptors can initiate two different forms of synaptic plasticity: long-term potentiation (LTP) and long-term depression (LTD). LTP arises when a single synapse is repeatedly stimulated. This stimulation causes a calcium- and CaMKII-dependent cellular cascade, which results in the insertion of more AMPA receptors into the postsynaptic membrane. The next time glutamate is released from the presynaptic cell, it will bind to both NMDA and the newly inserted AMPA receptors, thus depolarizing the membrane more efficiently. LTD occurs when few glutamate molecules bind to NMDA receptors at a synapse (due to a low firing rate of the presynaptic neuron). The calcium that does flow through NMDA receptors initiates a different calcineurin and protein phosphatase 1-dependent cascade, which results in the endocytosis of AMPA receptors.

This makes the postsynaptic neuron less responsive to glutamate released from the presynaptic neuron.

Section Summary

Neurons have charged membranes because there are different concentrations of ions inside and outside of the cell. Voltage-gated ion channels control the movement of ions into and out of a neuron. When a neuronal membrane is depolarized to at least the threshold of excitation, an action potential is fired. The action potential is then propagated along a myelinated axon to the axon terminals. In a chemical synapse, the action potential causes release of neurotransmitter molecules into the synaptic cleft. Through binding to postsynaptic receptors, the neurotransmitter can cause excitatory or inhibitory postsynaptic potentials by depolarizing or hyperpolarizing, respectively, the postsynaptic membrane. In electrical synapses, the action potential is directly communicated to the postsynaptic cell through gap junctions—large channel proteins that connect the pre-and postsynaptic membranes. Synapses are not static structures and can be strengthened and weakened. Two mechanisms of synaptic plasticity are long-term potentiation and long-term depression.

Art Connections

Exercise:

Problem:

[link] Potassium channel blockers, such as amiodarone and procainamide, which are used to treat abnormal electrical activity in the heart, called cardiac dysrhythmia, impede the movement of K+ through voltage-gated K+ channels. Which part of the action potential would you expect potassium channels to affect?

Solution:

[link] Potassium channel blockers slow the repolarization phase, but have no effect on depolarization.

Review Questions

Exercise:

Problem:

For a neuron to fire an action potential, its membrane must reach _____.

    a. hyperpolarization
    b. the threshold of excitation
    c. the refractory period
    d. inhibitory postsynaptic potential

Solution:

B

Exercise:

Problem:

After an action potential, the opening of additional voltage-gated _____ channels and the inactivation of sodium channels, cause the membrane to return to its resting membrane potential.

    a. sodium
    b. potassium
    c. calcium
    d. chloride

Solution:

B

Exercise:

Problem:

What is the term for protein channels that connect two neurons at an electrical synapse?

    a. synaptic vesicles
    b. voltage-gated ion channels
    c. gap junction protein
    d. sodium-potassium exchange pumps

Solution:

C

Free Response

Exercise:

Problem:

How does myelin aid propagation of an action potential along an axon? How do the nodes of Ranvier help this process?

Solution:

Myelin prevents the leak of current from the axon. Nodes of Ranvier allow the action potential to be regenerated at specific points along the axon. They also save energy for the cell since voltage-gated ion channels and sodium-potassium transporters are not needed along myelinated portions of the axon.

Exercise:

Problem: What are the main steps in chemical neurotransmission?

Solution:

An action potential travels along an axon until it depolarizes the membrane at an axon terminal. Depolarization of the membrane causes voltage-gated Ca^{2+} channels to open and Ca^{2+} to enter the cell. The intracellular calcium influx causes synaptic vesicles containing neurotransmitter to fuse with the presynaptic membrane. The neurotransmitter diffuses across the synaptic cleft and binds to receptors on the postsynaptic membrane. Depending on the specific neurotransmitter and postsynaptic receptor, this action can cause positive (excitatory postsynaptic potential) or negative (inhibitory postsynaptic potential) ions to enter the cell.

Glossary

action potential
    self-propagating momentary change in the electrical potential of a neuron (or muscle) membrane

depolarization
    change in the membrane potential to a less negative value

excitatory postsynaptic potential (EPSP)
    depolarization of a postsynaptic membrane caused by neurotransmitter molecules released from a presynaptic cell

hyperpolarization
    change in the membrane potential to a more negative value

inhibitory postsynaptic potential (IPSP)
    hyperpolarization of a postsynaptic membrane caused by neurotransmitter molecules released from a presynaptic cell

long-term depression (LTD)
    prolonged decrease in synaptic coupling between a pre- and postsynaptic cell

long-term potentiation (LTP)
    prolonged increase in synaptic coupling between a pre-and
    postsynaptic cell

membrane potential
    difference in electrical potential between the inside and outside of a
    cell

refractory period
    period after an action potential when it is more difficult or impossible
    for an action potential to be fired; caused by inactivation of sodium
    channels and activation of additional potassium channels of the
    membrane

saltatory conduction
    "jumping" of an action potential along an axon from one node of
    Ranvier to the next

summation
    process of multiple presynaptic inputs creating EPSPs around the same
    time for the postsynaptic neuron to be sufficiently depolarized to fire
    an action potential

synaptic cleft
    space between the presynaptic and postsynaptic membranes

synaptic vesicle
    spherical structure that contains a neurotransmitter

threshold of excitation
    level of depolarization needed for an action potential to fire

The Central Nervous System
By the end of this section, you will be able to:

- Identify the spinal cord, cerebral lobes, and other brain areas on a diagram of the brain
- Describe the basic functions of the spinal cord, cerebral lobes, and other brain areas

The central nervous system (CNS) is made up of the brain, a part of which is shown in [link] and spinal cord and is covered with three layers of protective coverings called **meninges** (from the Greek word for membrane). The outermost layer is the **dura mater** (Latin for "hard mother"). As the Latin suggests, the primary function for this thick layer is to protect the brain and spinal cord. The dura mater also contains vein-like structures that carry blood from the brain back to the heart. The middle layer is the web-like **arachnoid mater**. The last layer is the **pia mater** (Latin for "soft mother"), which directly contacts and covers the brain and spinal cord like plastic wrap. The space between the arachnoid and pia maters is filled with **cerebrospinal fluid (CSF)**. CSF is produced by a tissue called **choroid plexus** in fluid-filled compartments in the CNS called **ventricles**. The brain floats in CSF, which acts as a cushion and shock absorber and makes the brain neutrally buoyant. CSF also functions to circulate chemical substances throughout the brain and into the spinal cord.

The entire brain contains only about 8.5 tablespoons of CSF, but CSF is constantly produced in the ventricles. This creates a problem when a ventricle is blocked—the CSF builds up and creates swelling and the brain is pushed against the skull. This swelling condition is called hydrocephalus ("water head") and can cause seizures, cognitive problems, and even death if a shunt is not inserted to remove the fluid and pressure.
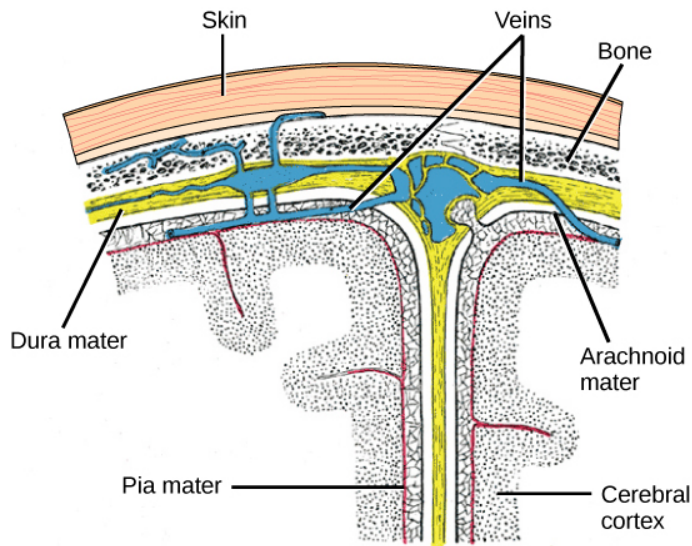
The cerebral cortex is covered by three layers of meninges: the dura, arachnoid, and pia maters. (credit: modification of work by Gray's Anatomy)

Brain

The brain is the part of the central nervous system that is contained in the cranial cavity of the skull. It includes the cerebral cortex, limbic system, basal ganglia, thalamus, hypothalamus, and cerebellum. There are three different ways that a brain can be sectioned in order to view internal structures: a sagittal section cuts the brain left to right, as shown in [link]**b**, a coronal section cuts the brain front to back, as shown in [link]**a**, and a horizontal section cuts the brain top to bottom.

Cerebral Cortex

The outermost part of the brain is a thick piece of nervous system tissue called the **cerebral cortex**, which is folded into hills called **gyri** (singular:

gyrus) and valleys called **sulci** (singular: sulcus). The cortex is made up of two hemispheres—right and left—which are separated by a large sulcus. A thick fiber bundle called the **corpus callosum** (Latin: "tough body") connects the two hemispheres and allows information to be passed from one side to the other. Although there are some brain functions that are localized more to one hemisphere than the other, the functions of the two hemispheres are largely redundant. In fact, sometimes (very rarely) an entire hemisphere is removed to treat severe epilepsy. While patients do suffer some deficits following the surgery, they can have surprisingly few problems, especially when the surgery is performed on children who have very immature nervous systems.
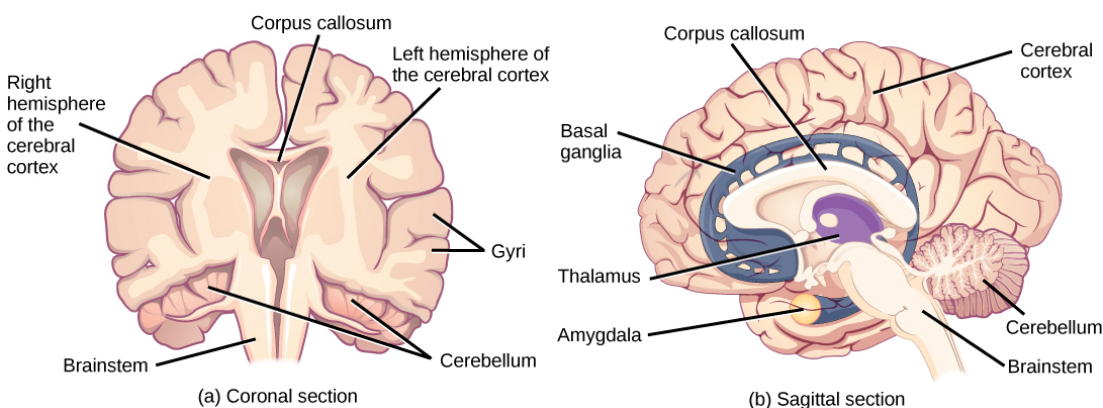
These illustrations show the (a) coronal and (b) sagittal sections of the human brain.

In other surgeries to treat severe epilepsy, the corpus callosum is cut instead of removing an entire hemisphere. This causes a condition called split-brain, which gives insights into unique functions of the two hemispheres. For example, when an object is presented to patients' left visual field, they may be unable to verbally name the object (and may claim to not have seen an object at all). This is because the visual input from the left visual field crosses and enters the right hemisphere and cannot then signal to the speech center, which generally is found in the left side of the brain. Remarkably, if a split-brain patient is asked to pick up a specific object out of a group of

objects with the left hand, the patient will be able to do so but will still be unable to vocally identify it.

Each cortical hemisphere contains regions called lobes that are involved in different functions. Scientists use various techniques to determine what brain areas are involved in different functions: they examine patients who have had injuries or diseases that affect specific areas and see how those areas are related to functional deficits. They also conduct animal studies where they stimulate brain areas and see if there are any behavioral changes. They use a technique called transmagnetic stimulation (TMS) to temporarily deactivate specific parts of the cortex using strong magnets placed outside the head; and they use functional magnetic resonance imaging (fMRI) to look at changes in oxygenated blood flow in particular brain regions that correlate with specific behavioral tasks. These techniques, and others, have given great insight into the functions of different brain regions but have also showed that any given brain area can be involved in more than one behavior or process, and any given behavior or process generally involves neurons in multiple brain areas. That being said, each hemisphere of the mammalian cerebral cortex can be broken down into four functionally and spatially defined lobes: frontal, parietal, temporal, and occipital. [link] illustrates these four lobes of the human cerebral cortex.
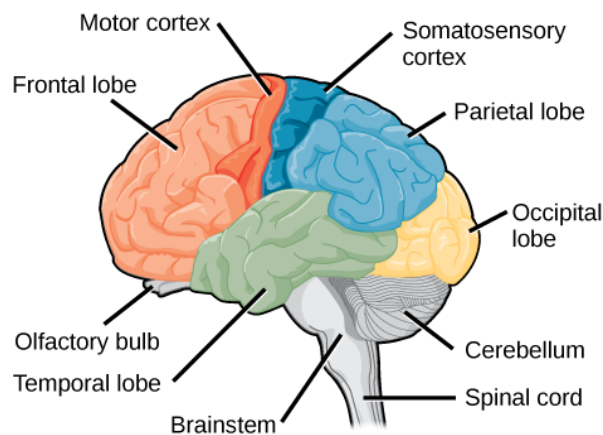
The human cerebral cortex
includes the frontal, parietal,
temporal, and occipital lobes.

The **frontal lobe** is located at the front of the brain, over the eyes. This lobe contains the olfactory bulb, which processes smells. The frontal lobe also contains the motor cortex, which is important for planning and implementing movement. Areas within the motor cortex map to different muscle groups, and there is some organization to this map, as shown in [link]. For example, the neurons that control movement of the fingers are next to the neurons that control movement of the hand. Neurons in the frontal lobe also control cognitive functions like maintaining attention, speech, and decision-making. Studies of humans who have damaged their frontal lobes show that parts of this area are involved in personality, socialization, and assessing risk.
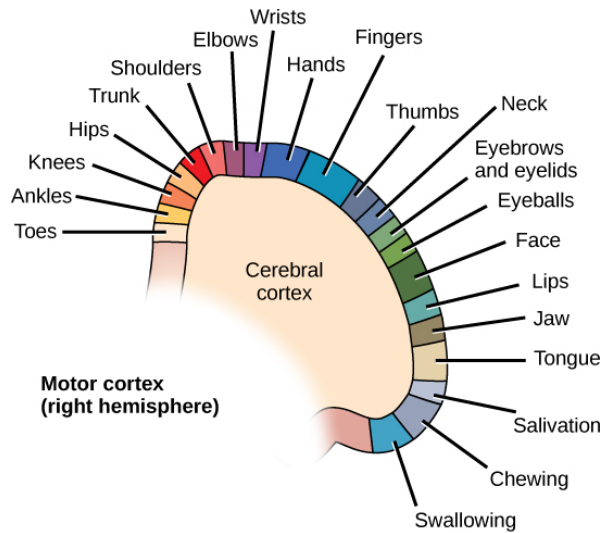
Different parts of the motor cortex control different muscle groups. Muscle groups that are neighbors in the body are generally controlled by neighboring regions of the motor cortex as well. For example, the neurons that control finger movement are near the neurons that control hand movement.

The **parietal lobe** is located at the top of the brain. Neurons in the parietal lobe are involved in speech and also reading. Two of the parietal lobe's main functions are processing **somatosensation**—touch sensations like pressure, pain, heat, cold—and processing **proprioception**—the sense of how parts of the body are oriented in space. The parietal lobe contains a somatosensory map of the body similar to the motor cortex.

The **occipital lobe** is located at the back of the brain. It is primarily involved in vision—seeing, recognizing, and identifying the visual world.

The **temporal lobe** is located at the base of the brain by your ears and is primarily involved in processing and interpreting sounds. It also contains the **hippocampus** (Greek for "seahorse")—a structure that processes memory formation. The hippocampus is illustrated in [link]. The role of the hippocampus in memory was partially determined by studying one famous epileptic patient, HM, who had both sides of his hippocampus removed in an attempt to cure his epilepsy. His seizures went away, but he could no longer form new memories (although he could remember some facts from before his surgery and could learn new motor tasks).

Note:
Evolution Connection
Cerebral Cortex
Compared to other vertebrates, mammals have exceptionally large brains for their body size. An entire alligator's brain, for example, would fill about one and a half teaspoons. This increase in brain to body size ratio is especially pronounced in apes, whales, and dolphins. While this increase in overall brain size doubtlessly played a role in the evolution of complex behaviors unique to mammals, it does not tell the whole story. Scientists have found a relationship between the relatively high surface area of the cortex and the intelligence and complex social behaviors exhibited by some mammals. This increased surface area is due, in part, to increased folding of the cortical sheet (more sulci and gyri). For example, a rat cortex is very smooth with very few sulci and gyri. Cat and sheep cortices have more sulci and gyri. Chimps, humans, and dolphins have even more.

Rat
Human
Cat
Chimpanzee
Dolphin
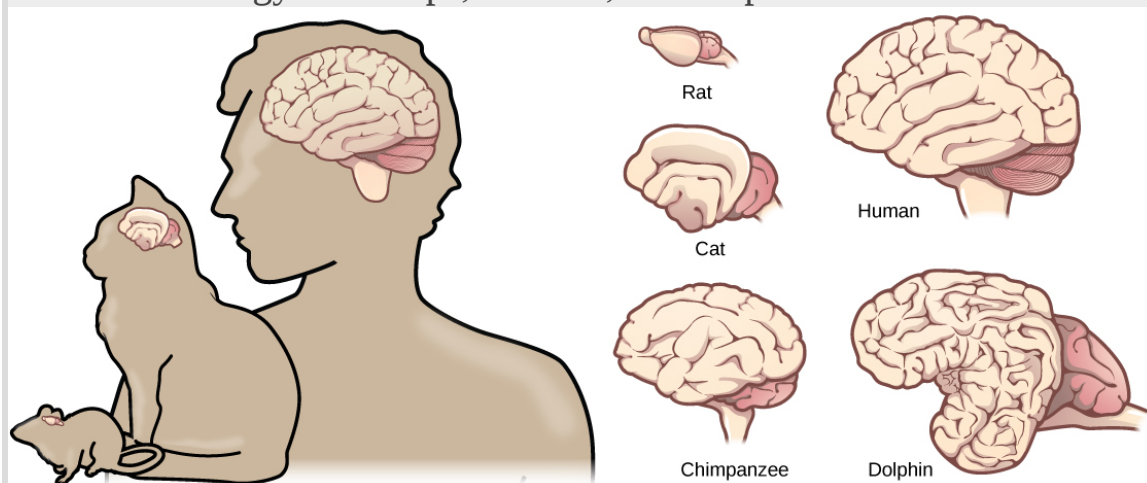
Mammals have larger brain-to-body ratios than other vertebrates. Within mammals, increased cortical folding and surface area is correlated with complex behavior.

Basal Ganglia

Interconnected brain areas called the **basal ganglia** (or **basal nuclei**), shown in [link]**b**, play important roles in movement control and posture. Damage to the basal ganglia, as in Parkinson's disease, leads to motor impairments like a shuffling gait when walking. The basal ganglia also regulate motivation. For example, when a wasp sting led to bilateral basal ganglia damage in a 25-year-old businessman, he began to spend all his days in bed and showed no interest in anything or anybody. But when he was externally stimulated—as when someone asked to play a card game with him—he was able to function normally. Interestingly, he and other similar patients do not report feeling bored or frustrated by their state.

Thalamus

The **thalamus** (Greek for "inner chamber"), illustrated in [link], acts as a gateway to and from the cortex. It receives sensory and motor inputs from the body and also receives feedback from the cortex. This feedback mechanism can modulate conscious awareness of sensory and motor inputs depending on the attention and arousal state of the animal. The thalamus helps regulate consciousness, arousal, and sleep states. A rare genetic disorder called fatal familial insomnia causes the degeneration of thalamic neurons and glia. This disorder prevents affected patients from being able to sleep, among other symptoms, and is eventually fatal.
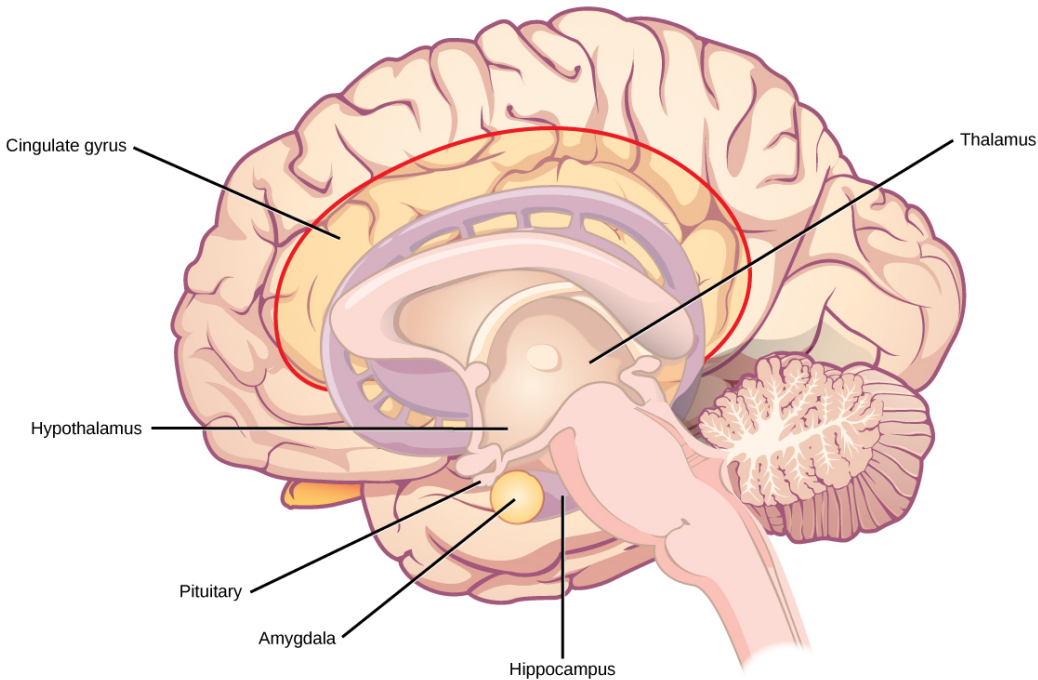
The limbic system regulates emotion and other behaviors. It includes parts of the cerebral cortex located near the center of the brain, including the cingulate gyrus and the hippocampus as well as the thalamus, hypothalamus and amygdala.

Hypothalamus

Below the thalamus is the **hypothalamus**, shown in [link]. The hypothalamus controls the endocrine system by sending signals to the pituitary gland, a pea-sized endocrine gland that releases several different hormones that affect other glands as well as other cells. This relationship means that the hypothalamus regulates important behaviors that are controlled by these hormones. The hypothalamus is the body's thermostat— it makes sure key functions like food and water intake, energy expenditure, and body temperature are kept at appropriate levels. Neurons within the

hypothalamus also regulate circadian rhythms, sometimes called sleep cycles.

Limbic System

The **limbic system** is a connected set of structures that regulates emotion, as well as behaviors related to fear and motivation. It plays a role in memory formation and includes parts of the thalamus and hypothalamus as well as the hippocampus. One important structure within the limbic system is a temporal lobe structure called the **amygdala** (Greek for "almond"), illustrated in [link]. The two amygdala are important both for the sensation of fear and for recognizing fearful faces. The **cingulate gyrus** helps regulate emotions and pain.

Cerebellum

The **cerebellum** (Latin for "little brain"), shown in [link], sits at the base of the brain on top of the brainstem. The cerebellum controls balance and aids in coordinating movement and learning new motor tasks.

Brainstem

The **brainstem**, illustrated in [link], connects the rest of the brain with the spinal cord. It consists of the midbrain, medulla oblongata, and the pons. Motor and sensory neurons extend through the brainstem allowing for the relay of signals between the brain and spinal cord. Ascending neural pathways cross in this section of the brain allowing the left hemisphere of the cerebrum to control the right side of the body and vice versa. The brainstem coordinates motor control signals sent from the brain to the body. The brainstem controls several important functions of the body including alertness, arousal, breathing, blood pressure, digestion, heart rate, swallowing, walking, and sensory and motor information integration.

Spinal Cord

Connecting to the brainstem and extending down the body through the spinal column is the **spinal cord**, shown in [link]. The spinal cord is a thick bundle of nerve tissue that carries information about the body to the brain and from the brain to the body. The spinal cord is contained within the bones of the vertebrate column but is able to communicate signals to and from the body through its connections with spinal nerves (part of the peripheral nervous system). A cross-section of the spinal cord looks like a white oval containing a gray butterfly-shape, as illustrated in [link]. Myelinated axons make up the "white matter" and neuron and glial cell bodies make up the "gray matter." Gray matter is also composed of interneurons, which connect two neurons each located in different parts of the body. Axons and cell bodies in the dorsal (facing the back of the animal) spinal cord convey mostly sensory information from the body to the brain. Axons and cell bodies in the ventral (facing the front of the animal) spinal cord primarily transmit signals controlling movement from the brain to the body.

The spinal cord also controls motor reflexes. These reflexes are quick, unconscious movements—like automatically removing a hand from a hot object. Reflexes are so fast because they involve local synaptic connections. For example, the knee reflex that a doctor tests during a routine physical is controlled by a single synapse between a sensory neuron and a motor neuron. While a reflex may only require the involvement of one or two synapses, synapses with interneurons in the spinal column transmit information to the brain to convey what happened (the knee jerked, or the hand was hot).

In the United States, there around 10,000 spinal cord injuries each year. Because the spinal cord is the information superhighway connecting the brain with the body, damage to the spinal cord can lead to paralysis. The extent of the paralysis depends on the location of the injury along the spinal cord and whether the spinal cord was completely severed. For example, if the spinal cord is damaged at the level of the neck, it can cause paralysis from the neck down, whereas damage to the spinal column further down may limit paralysis to the legs. Spinal cord injuries are notoriously difficult

to treat because spinal nerves do not regenerate, although ongoing research suggests that stem cell transplants may be able to act as a bridge to reconnect severed nerves. Researchers are also looking at ways to prevent the inflammation that worsens nerve damage after injury. One such treatment is to pump the body with cold saline to induce hypothermia. This cooling can prevent swelling and other processes that are thought to worsen spinal cord injuries.
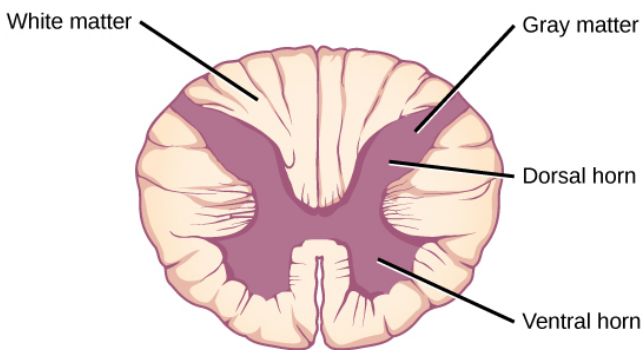
A cross-section of the spinal cord shows gray matter (containing cell bodies and interneurons) and white matter (containing axons).

Section Summary

The vertebrate central nervous system contains the brain and the spinal cord, which are covered and protected by three meninges. The brain contains structurally and functionally defined regions. In mammals, these include the cortex (which can be broken down into four primary functional lobes: frontal, temporal, occipital, and parietal), basal ganglia, thalamus, hypothalamus, limbic system, cerebellum, and brainstem—although structures in some of these designations overlap. While functions may be primarily localized to one structure in the brain, most complex functions, like language and sleep, involve neurons in multiple brain regions. The

spinal cord is the information superhighway that connects the brain with the rest of the body through its connections with peripheral nerves. It transmits sensory and motor input and also controls motor reflexes.

Review Questions

Exercise:

Problem: The _____ lobe contains the visual cortex.

a. frontal
b. parietal
c. temporal
d. occipital

Solution:

D

Exercise:

Problem: The _____ connects the two cerebral hemispheres.

a. limbic system
b. corpus callosum
c. cerebellum
d. pituitary

Solution:

B

Exercise:

Problem: Neurons in the _____ control motor reflexes.

a. thalamus
b. spinal cord
c. parietal lobe
d. hippocampus

Solution:

B

Free Response

Exercise:

Problem:

What methods can be used to determine the function of a particular brain region?

Solution:

To determine the function of a specific brain area, scientists can look at patients who have damage in that brain area and see what symptoms they exhibit. Researchers can disable the brain structure temporarily using transcranial magnetic stimulation. They can disable or remove the area in an animal model. fMRI can be used to correlate specific functions with increased blood flow to brain regions.

Exercise:

Problem: What are the main functions of the spinal cord?

Solution:

The spinal cord transmits sensory information from the body to the brain and motor commands from the brain to the body through its connections with peripheral nerves. It also controls motor reflexes.

Glossary

amygdala
>	structure within the limbic system that processes fear

arachnoid mater
>	spiderweb-like middle layer of the meninges that cover the central nervous system

basal ganglia
>	interconnected collections of cells in the brain that are involved in movement and motivation; also known as basal nuclei

basal nuclei
>	see basal ganglia

brainstem
>	portion of the brain that connects with the spinal cord; controls basic nervous system functions like breathing, heart rate, and swallowing

cerebellum
>	brain structure involved in posture, motor coordination, and learning new motor actions

cerebral cortex
>	outermost sheet of brain tissue; involved in many higher-order functions

choroid plexus
>	spongy tissue within ventricles that produces cerebrospinal fluid

cingulate gyrus
>	helps regulate emotions and pain; thought to directly drive the body's conscious response to unpleasant experiences

corpus callosum
>	thick fiber bundle that connects the cerebral hemispheres

cerebrospinal fluid (CSF)
    clear liquid that surrounds the brain and spinal cord and fills the
    ventricles and central canal; acts as a shock absorber and circulates
    material throughout the brain and spinal cord.

dura mater
    tough outermost layer that covers the central nervous system

frontal lobe
    part of the cerebral cortex that contains the motor cortex and areas
    involved in planning, attention, and language

gyrus
    (plural: gyri) ridged protrusions in the cortex

hippocampus
    brain structure in the temporal lobe involved in processing memories

hypothalamus
    brain structure that controls hormone release and body homeostasis

limbic system
    connected brain areas that process emotion and motivation

meninge
    membrane that covers and protects the central nervous system

occipital lobe
    part of the cerebral cortex that contains visual cortex and processes
    visual stimuli

parietal lobe
    part of the cerebral cortex involved in processing touch and the sense
    of the body in space

pia mater
    thin membrane layer directly covering the brain and spinal cord

proprioception

sense about how parts of the body are oriented in space

somatosensation
    sense of touch

spinal cord
    thick fiber bundle that connects the brain with peripheral nerves;
    transmits sensory and motor information; contains neurons that control
    motor reflexes

sulcus
    (plural: sulci) indents or "valleys" in the cortex

temporal lobe
    part of the cerebral cortex that processes auditory input; parts of the
    temporal lobe are involved in speech, memory, and emotion processing

thalamus
    brain area that relays sensory information to the cortex

ventricle
    cavity within brain that contains cerebrospinal fluid

The Peripheral Nervous System
By the end of this section, you will be able to:

- Describe the organization and functions of the sympathetic and parasympathetic nervous systems
- Describe the organization and function of the sensory-somatic nervous system

The peripheral nervous system (PNS) is the connection between the central nervous system and the rest of the body. The CNS is like the power plant of the nervous system. It creates the signals that control the functions of the body. The PNS is like the wires that go to individual houses. Without those "wires," the signals produced by the CNS could not control the body (and the CNS would not be able to receive sensory information from the body either).

The PNS can be broken down into the **autonomic nervous system**, which controls bodily functions without conscious control, and the **sensory-somatic nervous system**, which transmits sensory information from the skin, muscles, and sensory organs to the CNS and sends motor commands from the CNS to the muscles.

Autonomic Nervous System

Note:
Art Connection

Autonomic Nervous System

Parasympathetic

Preganglionic neuron: soma is usually in the brainstem or sacral (toward the bottom) spinal cord

Postganglionic neuron: soma is usually in a ganglion near the target organ

Neurotransmitters released from postganglionic synapse: acetylcholine or nitric oxide

Target organ

"Rest and digest" response is activated

Sympathetic

Neurotransmitter released from the preganglionic synapse: acetylcholine

Preganglionic neuron: soma is usually in the spine

Postganglionic neuron: soma is in a sympathetic ganglion, located next to the spinal cord

Neurotransmitters released from postganglionic synapse: norepinephrine

Target organ

"Fight or flight" response is activated

In the autonomic nervous system, a preganglionic neuron of the CNS synapses with a postganglionic neuron of the PNS. The postganglionic neuron, in turn, acts on a target organ. Autonomic responses are mediated by the sympathetic and the parasympathetic systems, which are antagonistic to one another. The sympathetic system activates the "fight or flight" response, while the parasympathetic system activates the "rest and digest" response.

Which of the following statements is false?

a. The parasympathetic pathway is responsible for resting the body, while the sympathetic pathway is responsible for preparing for an emergency.
b. Most preganglionic neurons in the sympathetic pathway originate in the spinal cord.
c. Slowing of the heartbeat is a parasympathetic response.
d. Parasympathetic neurons are responsible for releasing norepinephrine on the target organ, while sympathetic neurons are responsible for releasing acetylcholine.

The autonomic nervous system serves as the relay between the CNS and the internal organs. It controls the lungs, the heart, smooth muscle, and exocrine and endocrine glands. The autonomic nervous system controls these organs largely without conscious control; it can continuously monitor the conditions of these different systems and implement changes as needed. Signaling to the target tissue usually involves two synapses: a preganglionic neuron (originating in the CNS) synapses to a neuron in a ganglion that, in turn, synapses on the target organ, as illustrated in [link]. There are two divisions of the autonomic nervous system that often have opposing effects: the sympathetic nervous system and the parasympathetic nervous system.

Sympathetic Nervous System

The **sympathetic nervous system** is responsible for the "fight or flight" response that occurs when an animal encounters a dangerous situation. One way to remember this is to think of the surprise a person feels when encountering a snake ("snake" and "sympathetic" both begin with "s"). Examples of functions controlled by the sympathetic nervous system include an accelerated heart rate and inhibited digestion. These functions help prepare an organism's body for the physical strain required to escape a potentially dangerous situation or to fend off a predator.
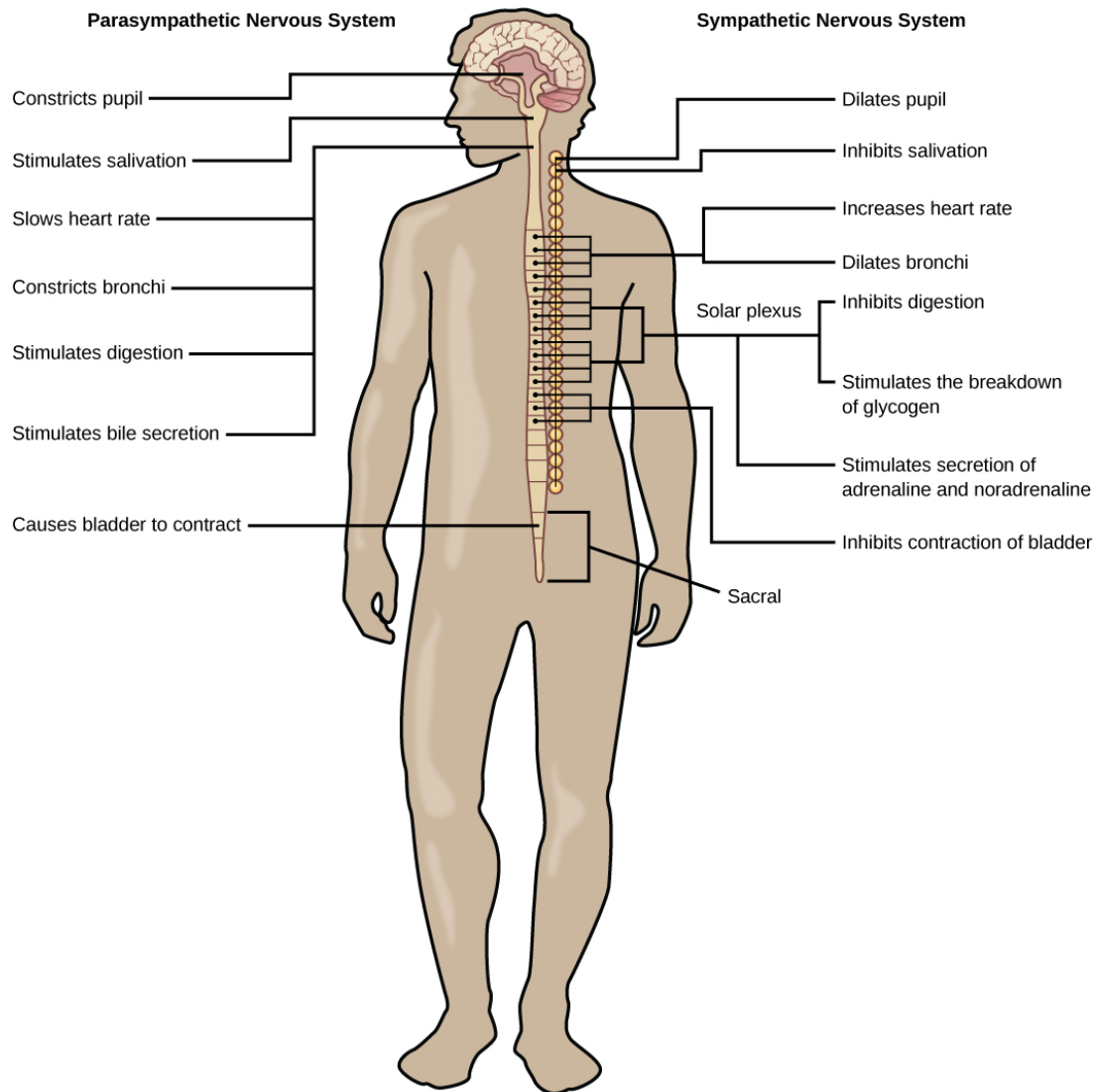
The sympathetic and parasympathetic nervous systems often have opposing effects on target organs.

Most preganglionic neurons in the sympathetic nervous system originate in the spinal cord, as illustrated in [link]. The axons of these neurons release **acetylcholine** on postganglionic neurons within sympathetic ganglia (the sympathetic ganglia form a chain that extends alongside the spinal cord). The acetylcholine activates the postganglionic neurons. Postganglionic neurons then release **norepinephrine** onto target organs. As anyone who has ever felt a rush before a big test, speech, or athletic event can attest, the

effects of the sympathetic nervous system are quite pervasive. This is both because one preganglionic neuron synapses on multiple postganglionic neurons, amplifying the effect of the original synapse, and because the adrenal gland also releases norepinephrine (and the closely related hormone epinephrine) into the blood stream. The physiological effects of this norepinephrine release include dilating the trachea and bronchi (making it easier for the animal to breathe), increasing heart rate, and moving blood from the skin to the heart, muscles, and brain (so the animal can think and run). The strength and speed of the sympathetic response helps an organism avoid danger, and scientists have found evidence that it may also increase LTP—allowing the animal to remember the dangerous situation and avoid it in the future.

Parasympathetic Nervous System

While the sympathetic nervous system is activated in stressful situations, the **parasympathetic nervous system** allows an animal to "rest and digest." One way to remember this is to think that during a restful situation like a picnic, the parasympathetic nervous system is in control ("picnic" and "parasympathetic" both start with "p"). Parasympathetic preganglionic neurons have cell bodies located in the brainstem and in the sacral (toward the bottom) spinal cord, as shown in [link]. The axons of the preganglionic neurons release acetylcholine on the postganglionic neurons, which are generally located very near the target organs. Most postganglionic neurons release acetylcholine onto target organs, although some release nitric oxide.

The parasympathetic nervous system resets organ function after the sympathetic nervous system is activated (the common adrenaline dump you feel after a 'fight-or-flight' event). Effects of acetylcholine release on target organs include slowing of heart rate, lowered blood pressure, and stimulation of digestion.

Sensory-Somatic Nervous System

The sensory-somatic nervous system is made up of cranial and spinal nerves and contains both sensory and motor neurons. Sensory neurons transmit sensory information from the skin, skeletal muscle, and sensory organs to the CNS. Motor neurons transmit messages about desired movement from the CNS to the muscles to make them contract. Without its sensory-somatic nervous system, an animal would be unable to process any information about its environment (what it sees, feels, hears, and so on) and could not control motor movements. Unlike the autonomic nervous system, which has two synapses between the CNS and the target organ, sensory and motor neurons have only one synapse—one ending of the neuron is at the organ and the other directly contacts a CNS neuron. Acetylcholine is the main neurotransmitter released at these synapses.

Humans have 12 **cranial nerves**, nerves that emerge from or enter the skull (cranium), as opposed to the spinal nerves, which emerge from the vertebral column. Each cranial nerve is accorded a name, which are detailed in [link]. Some cranial nerves transmit only sensory information. For example, the olfactory nerve transmits information about smells from the nose to the brainstem. Other cranial nerves transmit almost solely motor information. For example, the oculomotor nerve controls the opening and closing of the eyelid and some eye movements. Other cranial nerves contain a mix of sensory and motor fibers. For example, the glossopharyngeal nerve has a role in both taste (sensory) and swallowing (motor).
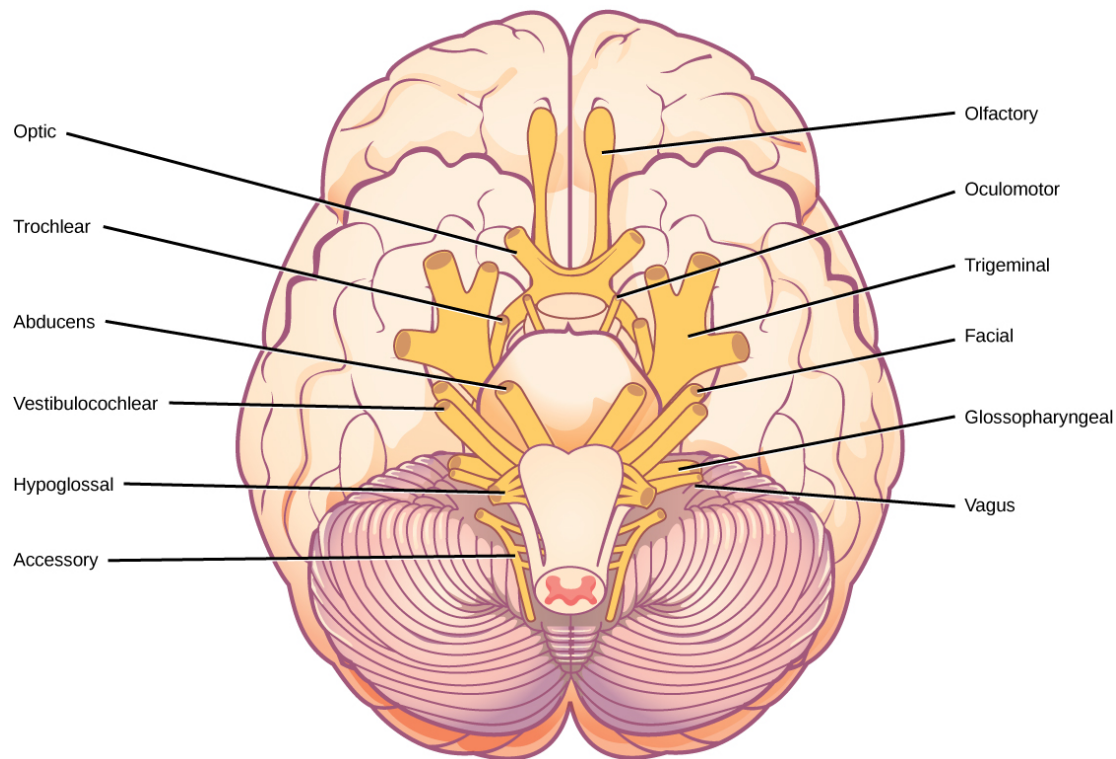
The human brain contains 12 cranial nerves that receive sensory input and control motor output for the head and neck.

Spinal nerves transmit sensory and motor information between the spinal cord and the rest of the body. Each of the 31 spinal nerves (in humans) contains both sensory and motor axons. The sensory neuron cell bodies are grouped in structures called dorsal root ganglia and are shown in [link]. Each sensory neuron has one projection—with a sensory receptor ending in skin, muscle, or sensory organs—and another that synapses with a neuron in the dorsal spinal cord. Motor neurons have cell bodies in the ventral gray matter of the spinal cord that project to muscle through the ventral root. These neurons are usually stimulated by interneurons within the spinal cord but are sometimes directly stimulated by sensory neurons.

White matter

Gray matter

Dorsal root

Dorsal root ganglion

Sensory neuron soma

Motor neuron soma

Ventral root

Spinal nerve

Cross Section of Spinal Cord
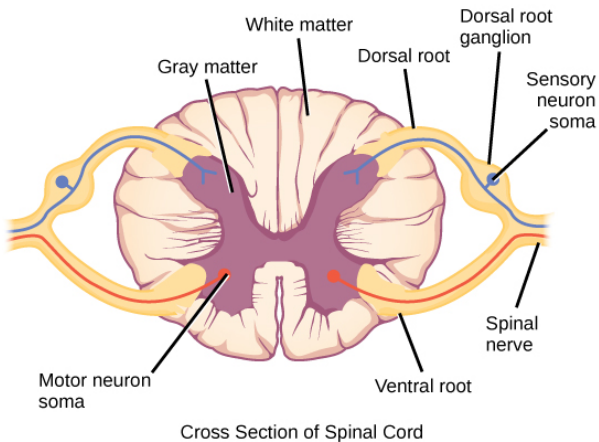
Spinal nerves contain both sensory and motor axons. The somas of sensory neurons are located in dorsal root ganglia. The somas of motor neurons are found in the ventral portion of the gray matter of the spinal cord.

Section Summary

The peripheral nervous system contains both the autonomic and sensory-somatic nervous systems. The autonomic nervous system provides unconscious control over visceral functions and has two divisions: the sympathetic and parasympathetic nervous systems. The sympathetic nervous system is activated in stressful situations to prepare the animal for a "fight or flight" response. The parasympathetic nervous system is active during restful periods. The sensory-somatic nervous system is made of cranial and spinal nerves that transmit sensory information from skin and muscle to the CNS and motor commands from the CNS to the muscles.

## Art Connections

Exercise:

Problem: [link] Which of the following statements is false?

    a. The parasympathetic pathway is responsible for relaxing the body, while the sympathetic pathway is responsible for preparing for an emergency.

    b. Most preganglionic neurons in the sympathetic pathway originate in the spinal cord.

    c. Slowing of the heartbeat is a parasympathetic response.

    d. Parasympathetic neurons are responsible for releasing norepinephrine on the target organ, while sympathetic neurons are responsible for releasing acetylcholine.

Solution:

[link] D

Review Questions

Exercise:

Problem: Activation of the sympathetic nervous system causes:

    a. increased blood flow into the skin

    b. a decreased heart rate

    c. an increased heart rate

    d. increased digestion

Solution:

C

Exercise:

Problem:

Where are parasympathetic preganglionic cell bodies located?

    a. cerebellum
    b. brainstem
    c. dorsal root ganglia
    d. skin

Solution:

B

Exercise:

Problem:_____ is released by motor nerve endings onto muscle.

    a. Acetylcholine
    b. Norepinephrine
    c. Dopamine
    d. Serotonin

Solution:

A

Free Response

Exercise:

Problem:

What are the main differences between the sympathetic and parasympathetic branches of the autonomic nervous system?

Solution:

The sympathetic nervous system prepares the body for "fight or flight," whereas the parasympathetic nervous system allows the body to "rest and digest." Sympathetic neurons release norepinephrine onto target organs; parasympathetic neurons release acetylcholine. Sympathetic neuron cell bodies are located in sympathetic ganglia. Parasympathetic neuron cell bodies are located in the brainstem and sacral spinal cord. Activation of the sympathetic nervous system increases heart rate and blood pressure and decreases digestion and blood flow to the skin. Activation of the parasympathetic nervous system decreases heart rate and blood pressure and increases digestion and blood flow to the skin.

Exercise:

Problem:

What are the main functions of the sensory-somatic nervous system?

Solution:

The sensory-somatic nervous system transmits sensory information from the skin, muscles, and sensory organs to the CNS. It also sends motor commands from the CNS to the muscles, causing them to contract.

Glossary

acetylcholine
    neurotransmitter released by neurons in the central nervous system and peripheral nervous system

autonomic nervous system
    part of the peripheral nervous system that controls bodily functions

cranial nerve
    sensory and/or motor nerve that emanates from the brain

norepinephrine

neurotransmitter and hormone released by activation of the
sympathetic nervous system

parasympathetic nervous system
division of autonomic nervous system that regulates visceral functions
during rest and digestion

sensory-somatic nervous system
system of sensory and motor nerves

spinal nerve
nerve projecting between skin or muscle and spinal cord

sympathetic nervous system
division of autonomic nervous system activated during stressful "fight
or flight" situations

Nervous System Disorders
By the end of this section, you will be able to:

- Describe the symptoms, potential causes, and treatment of several examples of nervous system disorders

A nervous system that functions correctly is a fantastically complex, well-oiled machine—synapses fire appropriately, muscles move when needed, memories are formed and stored, and emotions are well regulated. Unfortunately, each year millions of people in the United States deal with some sort of nervous system disorder. While scientists have discovered potential causes of many of these diseases, and viable treatments for some, ongoing research seeks to find ways to better prevent and treat all of these disorders.

Neurodegenerative Disorders

Neurodegenerative disorders are illnesses characterized by a loss of nervous system functioning that are usually caused by neuronal death. These diseases generally worsen over time as more and more neurons die. The symptoms of a particular neurodegenerative disease are related to where in the nervous system the death of neurons occurs. Spinocerebellar ataxia, for example, leads to neuronal death in the cerebellum. The death of these neurons causes problems in balance and walking. Neurodegenerative disorders include Huntington's disease, amyotrophic lateral sclerosis, Alzheimer's disease and other types of dementia disorders, and Parkinson's disease. Here, Alzheimer's and Parkinson's disease will be discussed in more depth.

Alzheimer's Disease

Alzheimer's disease is the most common cause of dementia in the elderly. In 2012, an estimated 5.4 million Americans suffered from Alzheimer's disease, and payments for their care are estimated at $200 billion. Roughly one in every eight people age 65 or older has the disease. Due to the aging

of the baby-boomer generation, there are projected to be as many as 13 million Alzheimer's patients in the United States in the year 2050.

Symptoms of Alzheimer's disease include disruptive memory loss, confusion about time or place, difficulty planning or executing tasks, poor judgment, and personality changes. Problems smelling certain scents can also be indicative of Alzheimer's disease and may serve as an early warning sign. Many of these symptoms are also common in people who are aging normally, so it is the severity and longevity of the symptoms that determine whether a person is suffering from Alzheimer's.

Alzheimer's disease was named for Alois Alzheimer, a German psychiatrist who published a report in 1911 about a woman who showed severe dementia symptoms. Along with his colleagues, he examined the woman's brain following her death and reported the presence of abnormal clumps, which are now called amyloid plaques, along with tangled brain fibers called neurofibrillary tangles. Amyloid plaques, neurofibrillary tangles, and an overall shrinking of brain volume are commonly seen in the brains of Alzheimer's patients. Loss of neurons in the hippocampus is especially severe in advanced Alzheimer's patients. [link] compares a normal brain to the brain of an Alzheimer's patient. Many research groups are examining the causes of these hallmarks of the disease.

One form of the disease is usually caused by mutations in one of three known genes. This rare form of early onset Alzheimer's disease affects fewer than five percent of patients with the disease and causes dementia beginning between the ages of 30 and 60. The more prevalent, late-onset form of the disease likely also has a genetic component. One particular gene, apolipoprotein E (APOE) has a variant (E4) that increases a carrier's likelihood of getting the disease. Many other genes have been identified that might be involved in the pathology.

Note:
Link to Learning

Visit [this website](#) for video links discussing genetics and Alzheimer's disease.

Unfortunately, there is no cure for Alzheimer's disease. Current treatments focus on managing the symptoms of the disease. Because decrease in the activity of cholinergic neurons (neurons that use the neurotransmitter acetylcholine) is common in Alzheimer's disease, several drugs used to treat the disease work by increasing acetylcholine neurotransmission, often by inhibiting the enzyme that breaks down acetylcholine in the synaptic cleft. Other clinical interventions focus on behavioral therapies like psychotherapy, sensory therapy, and cognitive exercises. Since Alzheimer's disease appears to hijack the normal aging process, research into prevention is prevalent. Smoking, obesity, and cardiovascular problems may be risk factors for the disease, so treatments for those may also help to prevent Alzheimer's disease. Some studies have shown that people who remain intellectually active by playing games, reading, playing musical instruments, and being socially active in later life have a reduced risk of developing the disease.
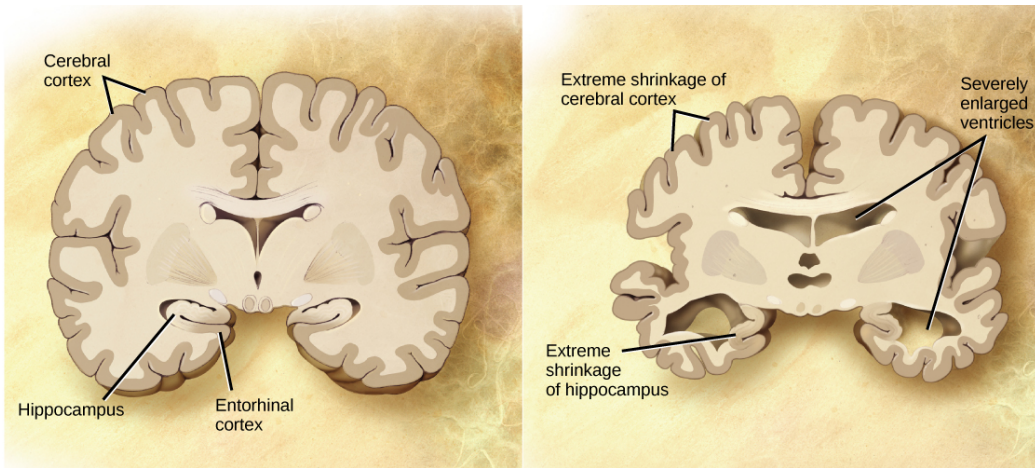
Compared to a normal brain (left), the brain from a patient with Alzheimer's disease (right) shows a dramatic neurodegeneration, particularly within the ventricles and hippocampus. (credit: modification of work by "Garrando"/Wikimedia Commons based on original images by ADEAR: "Alzheimer's Disease Education and Referral Center, a service of the National Institute on Aging")

Parkinson's Disease

Like Alzheimer's disease, **Parkinson's disease** is a neurodegenerative disease. It was first characterized by James Parkinson in 1817. Each year, 50,000-60,000 people in the United States are diagnosed with the disease. Parkinson's disease causes the loss of dopamine neurons in the substantia nigra, a midbrain structure that regulates movement. Loss of these neurons causes many symptoms including tremor (shaking of fingers or a limb), slowed movement, speech changes, balance and posture problems, and rigid muscles. The combination of these symptoms often causes a characteristic slow hunched shuffling walk, illustrated in [link]. Patients with Parkinson's disease can also exhibit psychological symptoms, such as dementia or emotional problems.

Although some patients have a form of the disease known to be caused by a single mutation, for most patients the exact causes of Parkinson's disease remain unknown: the disease likely results from a combination of genetic and environmental factors (similar to Alzheimer's disease). Post-mortem analysis of brains from Parkinson's patients shows the presence of Lewy bodies—abnormal protein clumps—in dopaminergic neurons. The prevalence of these Lewy bodies often correlates with the severity of the disease.

There is no cure for Parkinson's disease, and treatment is focused on easing symptoms. One of the most commonly prescribed drugs for Parkinson's is L-DOPA, which is a chemical that is converted into dopamine by neurons in the brain. This conversion increases the overall level of dopamine neurotransmission and can help compensate for the loss of dopaminergic neurons in the substantia nigra. Other drugs work by inhibiting the enzyme that breaks down dopamine.

Parkinson's patients often have a characteristic hunched walk.

Neurodevelopmental Disorders

Neurodevelopmental disorders occur when the development of the nervous system is disturbed. There are several different classes of neurodevelopmental disorders. Some, like Down Syndrome, cause intellectual deficits. Others specifically affect communication, learning, or the motor system. Some disorders like autism spectrum disorder and attention deficit/hyperactivity disorder have complex symptoms.

Autism

Autism spectrum disorder (ASD) is a neurodevelopmental disorder. Its severity differs from person to person. Estimates for the prevalence of the disorder have changed rapidly in the past few decades. Current estimates suggest that one in 88 children will develop the disorder. ASD is four times more prevalent in males than females.

> **Note:**
> Link to Learning
>
>
>
> [This video](#) discusses possible reasons why there has been a recent increase in the number of people diagnosed with autism.

A characteristic symptom of ASD is impaired social skills. Children with autism may have difficulty making and maintaining eye contact and reading social cues. They also may have problems feeling empathy for others. Other

symptoms of ASD include repetitive motor behaviors (such as rocking back and forth), preoccupation with specific subjects, strict adherence to certain rituals, and unusual language use. Up to 30 percent of patients with ASD develop epilepsy, and patients with some forms of the disorder (like Fragile X) also have intellectual disability. Because it is a spectrum disorder, other ASD patients are very functional and have good-to-excellent language skills. Many of these patients do not feel that they suffer from a disorder and instead think that their brains just process information differently.

Except for some well-characterized, clearly genetic forms of autism (like Fragile X and Rett's Syndrome), the causes of ASD are largely unknown. Variants of several genes correlate with the presence of ASD, but for any given patient, many different mutations in different genes may be required for the disease to develop. At a general level, ASD is thought to be a disease of "incorrect" wiring. Accordingly, brains of some ASD patients lack the same level of synaptic pruning that occurs in non-affected people. In the 1990s, a research paper linked autism to a common vaccine given to children. This paper was retracted when it was discovered that the author falsified data, and follow-up studies showed no connection between vaccines and autism.

Treatment for autism usually combines behavioral therapies and interventions, along with medications to treat other disorders common to people with autism (depression, anxiety, obsessive compulsive disorder). Although early interventions can help mitigate the effects of the disease, there is currently no cure for ASD.

Attention Deficit Hyperactivity Disorder (ADHD)

Approximately three to five percent of children and adults are affected by **attention deficit/hyperactivity disorder (ADHD)**. Like ASD, ADHD is more prevalent in males than females. Symptoms of the disorder include inattention (lack of focus), executive functioning difficulties, impulsivity, and hyperactivity beyond what is characteristic of the normal developmental stage. Some patients do not have the hyperactive component of symptoms and are diagnosed with a subtype of ADHD: attention deficit

disorder (ADD). Many people with ADHD also show comorbitity, in that they develop secondary disorders in addition to ADHD. Examples include depression or obsessive compulsive disorder (OCD). [link] provides some statistics concerning comorbidity with ADHD.

The cause of ADHD is unknown, although research points to a delay and dysfunction in the development of the prefrontal cortex and disturbances in neurotransmission. According to studies of twins, the disorder has a strong genetic component. There are several candidate genes that may contribute to the disorder, but no definitive links have been discovered. Environmental factors, including exposure to certain pesticides, may also contribute to the development of ADHD in some patients. Treatment for ADHD often involves behavioral therapies and the prescription of stimulant medications, which paradoxically cause a calming effect in these patients.
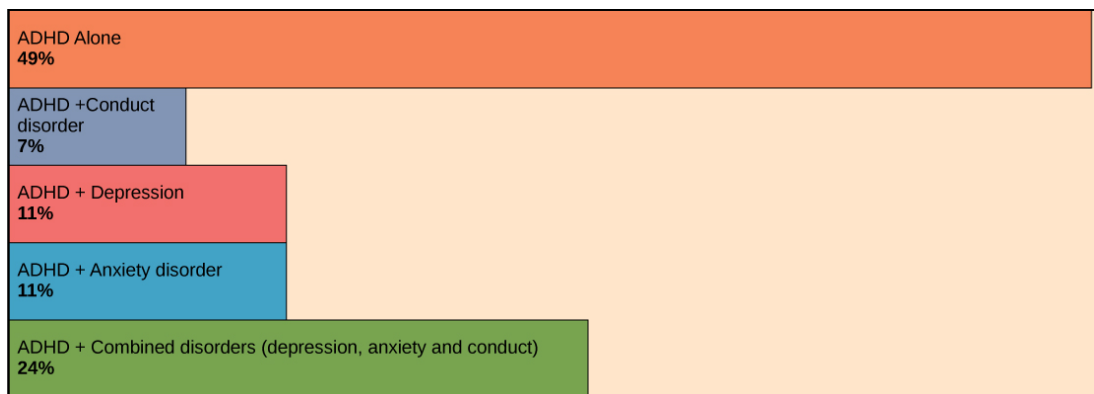
Many people with ADHD have one or more other neurological disorders. (credit "chart design and illustration": modification of work by Leigh Coriale; credit "data": Drs. Biederman and Faraone, Massachusetts General Hospital).

Note:
Career Connection

Neurologist

Neurologists are physicians who specialize in disorders of the nervous system. They diagnose and treat disorders such as epilepsy, stroke, dementia, nervous system injuries, Parkinson's disease, sleep disorders, and multiple sclerosis. Neurologists are medical doctors who have attended college, medical school, and completed three to four years of neurology residency.

When examining a new patient, a neurologist takes a full medical history and performs a complete physical exam. The physical exam contains specific tasks that are used to determine what areas of the brain, spinal cord, or peripheral nervous system may be damaged. For example, to check whether the hypoglossal nerve is functioning correctly, the neurologist will ask the patient to move his or her tongue in different ways. If the patient does not have full control over tongue movements, then the hypoglossal nerve may be damaged or there may be a lesion in the brainstem where the cell bodies of these neurons reside (or there could be damage to the tongue muscle itself).

Neurologists have other tools besides a physical exam they can use to diagnose particular problems in the nervous system. If the patient has had a seizure, for example, the neurologist can use electroencephalography (EEG), which involves taping electrodes to the scalp to record brain activity, to try to determine which brain regions are involved in the seizure. In suspected stroke patients, a neurologist can use a computerized tomography (CT) scan, which is a type of X-ray, to look for bleeding in the brain or a possible brain tumor. To treat patients with neurological problems, neurologists can prescribe medications or refer the patient to a neurosurgeon for surgery.

Note:
Link to Learning

[This website](#) allows you to see the different tests a neurologist might use to see what regions of the nervous system may be damaged in a patient.

Mental Illnesses

Mental illnesses are nervous system disorders that result in problems with thinking, mood, or relating with other people. These disorders are severe enough to affect a person's quality of life and often make it difficult for people to perform the routine tasks of daily living. Debilitating mental disorders plague approximately 12.5 million Americans (about 1 in 17 people) at an annual cost of more than $300 billion. There are several types of mental disorders including schizophrenia, major depression, bipolar disorder, anxiety disorders and phobias, post-traumatic stress disorders, and obsessive-compulsive disorder (OCD), among others. The American Psychiatric Association publishes the Diagnostic and Statistical Manual of Mental Disorders (or DSM), which describes the symptoms required for a patient to be diagnosed with a particular mental disorder. Each newly released version of the DSM contains different symptoms and classifications as scientists learn more about these disorders, their causes, and how they relate to each other. A more detailed discussion of two mental illnesses—schizophrenia and major depression—is given below.

Schizophrenia

Schizophrenia is a serious and often debilitating mental illness affecting one percent of people in the United States. Symptoms of the disease include the inability to differentiate between reality and imagination, inappropriate and unregulated emotional responses, difficulty thinking, and problems with

social situations. People with schizophrenia can suffer from hallucinations and hear voices; they may also suffer from delusions. Patients also have so-called "negative" symptoms like a flattened emotional state, loss of pleasure, and loss of basic drives. Many schizophrenic patients are diagnosed in their late adolescence or early 20s. The development of schizophrenia is thought to involve malfunctioning dopaminergic neurons and may also involve problems with glutamate signaling. Treatment for the disease usually requires antipsychotic medications that work by blocking dopamine receptors and decreasing dopamine neurotransmission in the brain. This decrease in dopamine can cause Parkinson's disease-like symptoms in some patients. While some classes of antipsychotics can be quite effective at treating the disease, they are not a cure, and most patients must remain medicated for the rest of their lives.

Depression

Major depression affects approximately 6.7 percent of the adults in the United States each year and is one of the most common mental disorders. To be diagnosed with major depressive disorder, a person must have experienced a severely depressed mood lasting longer than two weeks along with other symptoms including a loss of enjoyment in activities that were previously enjoyed, changes in appetite and sleep schedules, difficulty concentrating, feelings of worthlessness, and suicidal thoughts. The exact causes of major depression are unknown and likely include both genetic and environmental risk factors. Some research supports the "classic monoamine hypothesis," which suggests that depression is caused by a decrease in norepinephrine and serotonin neurotransmission. One argument against this hypothesis is the fact that some antidepressant medications cause an increase in norepinephrine and serotonin release within a few hours of beginning treatment—but clinical results of these medications are not seen until weeks later. This has led to alternative hypotheses: for example, dopamine may also be decreased in depressed patients, or it may actually be an increase in norepinephrine and serotonin that causes the disease, and antidepressants force a feedback loop that decreases this release. Treatments for depression include psychotherapy, electroconvulsive therapy, deep-brain stimulation, and prescription medications. There are several classes of

antidepressant medications that work through different mechanisms. For example, monoamine oxidase inhibitors (MAO inhibitors) block the enzyme that degrades many neurotransmitters (including dopamine, serotonin, norepinephrine), resulting in increased neurotransmitter in the synaptic cleft. Selective serotonin reuptake inhibitors (SSRIs) block the reuptake of serotonin into the presynaptic neuron. This blockage results in an increase in serotonin in the synaptic cleft. Other types of drugs such as norepinephrine-dopamine reuptake inhibitors and norepinephrine-serotonin reuptake inhibitors are also used to treat depression.

Other Neurological Disorders

There are several other neurological disorders that cannot be easily placed in the above categories. These include chronic pain conditions, cancers of the nervous system, epilepsy disorders, and stroke. Epilepsy and stroke are discussed below.

Epilepsy

Estimates suggest that up to three percent of people in the United States will be diagnosed with **epilepsy** in their lifetime. While there are several different types of epilepsy, all are characterized by recurrent seizures. Epilepsy itself can be a symptom of a brain injury, disease, or other illness. For example, people who have intellectual disability or ASD can experience seizures, presumably because the developmental wiring malfunctions that caused their disorders also put them at risk for epilepsy. For many patients, however, the cause of their epilepsy is never identified and is likely to be a combination of genetic and environmental factors. Often, seizures can be controlled with anticonvulsant medications. However, for very severe cases, patients may undergo brain surgery to remove the brain area where seizures originate.

Stroke

A stroke results when blood fails to reach a portion of the brain for a long enough time to cause damage. Without the oxygen supplied by blood flow, neurons in this brain region die. This neuronal death can cause many different symptoms—depending on the brain area affected— including headache, muscle weakness or paralysis, speech disturbances, sensory problems, memory loss, and confusion. Stroke is often caused by blood clots and can also be caused by the bursting of a weak blood vessel. Strokes are extremely common and are the third most common cause of death in the United States. On average one person experiences a stroke every 40 seconds in the United States. Approximately 75 percent of strokes occur in people older than 65. Risk factors for stroke include high blood pressure, diabetes, high cholesterol, and a family history of stroke. Smoking doubles the risk of stroke. Because a stroke is a medical emergency, patients with symptoms of a stroke should immediately go to the emergency room, where they can receive drugs that will dissolve any clot that may have formed. These drugs will not work if the stroke was caused by a burst blood vessel or if the stroke occurred more than three hours before arriving at the hospital. Treatment following a stroke can include blood pressure medication (to prevent future strokes) and (sometimes intense) physical therapy.

Section Summary

Some general themes emerge from the sampling of nervous system disorders presented above. The causes for most disorders are not fully understood—at least not for all patients—and likely involve a combination of nature (genetic mutations that become risk factors) and nurture (emotional trauma, stress, hazardous chemical exposure). Because the causes have yet to be fully determined, treatment options are often lacking and only address symptoms.

Review Questions

Exercise:

Problem:

Parkinson's disease is a caused by the degeneration of neurons that release _____.

    a. serotonin
    b. dopamine
    c. glutamate
    d. norepinephrine

Solution:

B

Exercise:

Problem:

_____ medications are often used to treat patients with ADHD.

    a. Tranquilizer
    b. Antibiotic
    c. Stimulant
    d. Anti-seizure

Solution:

C

Exercise:

Problem: Strokes are often caused by _____.

    a. neurodegeneration
    b. blood clots or burst blood vessels
    c. seizures
    d. viruses

Solution:

B

Free Response

Exercise:

Problem: What are the main symptoms of Alzheimer's disease?

Solution:

Symptoms of Alzheimer's disease include disruptive memory loss, confusion about time or place, difficulties planning or executing tasks, poor judgment, and personality changes.

Exercise:

Problem:

What are possible treatments for patients with major depression?

Solution:

Possible treatments for patients with major depression include psychotherapy and prescription medications. MAO inhibitor drugs inhibit the breakdown of certain neurotransmitters (including dopamine, serotonin, norepinephrine) in the synaptic cleft. SSRI medications inhibit the reuptake of serotonin into the presynaptic neuron.

Glossary

Alzheimer's disease
　　neurodegenerative disorder characterized by problems with memory and thinking

attention deficit hyperactivity disorder (ADHD)
    neurodevelopmental disorder characterized by difficulty maintaining
    attention and controlling impulses

autism spectrum disorder (ASD)
    neurodevelopmental disorder characterized by impaired social
    interaction and communication abilities

epilepsy
    neurological disorder characterized by recurrent seizures

major depression
    mental illness characterized by prolonged periods of sadness

neurodegenerative disorder
    nervous system disorder characterized by the progressive loss of
    neurological functioning, usually caused by neuron death

Parkinson's disease
    neurodegenerative disorder that affects the control of movement

schizophrenia
    mental disorder characterized by the inability to accurately perceive
    reality; patients often have difficulty thinking clearly and can suffer
    from delusions

Introduction class="introduction"

This shark uses its senses of sight, vibration (lateral-line system), and smell to hunt, but it also relies on its ability to sense the electric fields of prey, a sense not present in most land animals. (credit: modification of work by Hermanus Backpackers Hostel, South Africa)

In more advanced animals, the senses are constantly at work, making the animal aware of stimuli—such as light, or sound, or the presence of a chemical substance in the external environment—and monitoring information about the organism's internal environment. All bilaterally symmetric animals have a sensory system, and the development of any species' sensory system has been driven by natural selection; thus, sensory systems differ among species according to the demands of their environments. The shark, unlike most fish predators, is electrosensitive—that is, sensitive to electrical fields produced by other animals in its environment. While it is helpful to this underwater predator, electrosensitivity is a sense not found in most land animals.

Sensory Processes
By the end of this section, you will be able to:

- Identify the general and special senses in humans
- Describe three important steps in sensory perception
- Explain the concept of just-noticeable difference in sensory perception

Senses provide information about the body and its environment. Humans have five special senses: olfaction (smell), gustation (taste), equilibrium (balance and body position), vision, and hearing. Additionally, we possess general senses, also called somatosensation, which respond to stimuli like temperature, pain, pressure, and vibration. **Vestibular sensation**, which is an organism's sense of spatial orientation and balance, **proprioception** (position of bones, joints, and muscles), and the sense of limb position that is used to track **kinesthesia** (limb movement) are part of somatosensation. Although the sensory systems associated with these senses are very different, all share a common function: to convert a stimulus (such as light, or sound, or the position of the body) into an electrical signal in the nervous system. This process is called **sensory transduction**.

There are two broad types of cellular systems that perform sensory transduction. In one, a neuron works with a **sensory receptor**, a cell, or cell process that is specialized to engage with and detect a specific stimulus. Stimulation of the sensory receptor activates the associated afferent neuron, which carries information about the stimulus to the central nervous system. In the second type of sensory transduction, a sensory nerve ending responds to a stimulus in the internal or external environment: this neuron constitutes the sensory receptor. Free nerve endings can be stimulated by several different stimuli, thus showing little receptor specificity. For example, pain receptors in your gums and teeth may be stimulated by temperature changes, chemical stimulation, or pressure.

Reception

The first step in sensation is **reception**, which is the activation of sensory receptors by stimuli such as mechanical stimuli (being bent or squished, for example), chemicals, or temperature. The receptor can then respond to the

stimuli. The region in space in which a given sensory receptor can respond to a stimulus, be it far away or in contact with the body, is that receptor's **receptive field**. Think for a moment about the differences in receptive fields for the different senses. For the sense of touch, a stimulus must come into contact with body. For the sense of hearing, a stimulus can be a moderate distance away (some baleen whale sounds can propagate for many kilometers). For vision, a stimulus can be very far away; for example, the visual system perceives light from stars at enormous distances.

Transduction

The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system. This takes place at the sensory receptor, and the change in electrical potential that is produced is called the **receptor potential**. How is sensory input, such as pressure on the skin, changed to a receptor potential? In this example, a type of receptor called a **mechanoreceptor** (as shown in [link]) possesses specialized membranes that respond to pressure. Disturbance of these dendrites by compressing them or bending them opens gated ion channels in the plasma membrane of the sensory neuron, changing its electrical potential. Recall that in the nervous system, a positive change of a neuron's electrical potential (also called the membrane potential), depolarizes the neuron. Receptor potentials are graded potentials: the magnitude of these graded (receptor) potentials varies with the strength of the stimulus. If the magnitude of depolarization is sufficient (that is, if membrane potential reaches a threshold), the neuron will fire an action potential. In most cases, the correct stimulus impinging on a sensory receptor will drive membrane potential in a positive direction, although for some receptors, such as those in the visual system, this is not always the case.
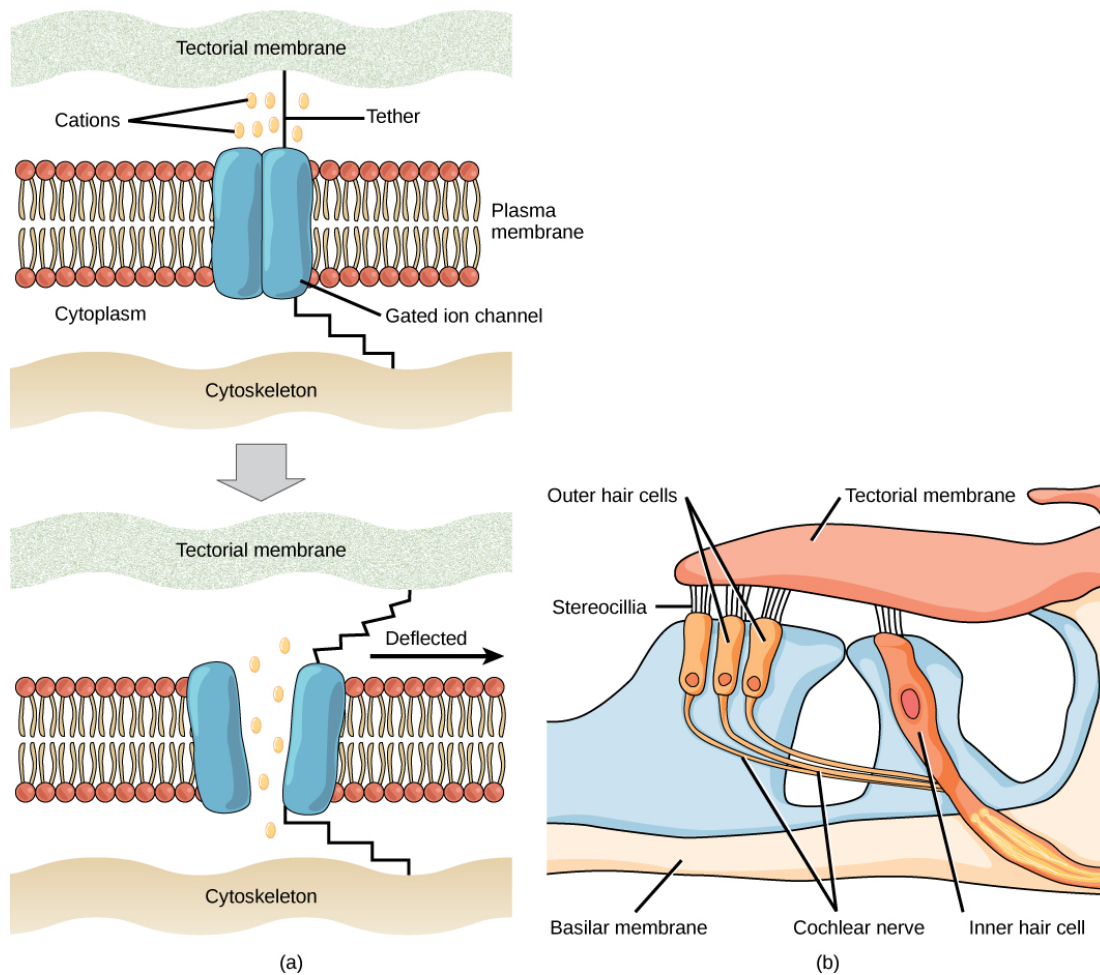
(a) Mechanosensitive ion channels are gated ion channels that respond to mechanical deformation of the plasma membrane. A mechanosensitive channel is connected to the plasma membrane and the cytoskeleton by hair-like tethers. When pressure causes the extracellular matrix to move, the channel opens, allowing ions to enter or exit the cell. (b) Stereocilia in the human ear are connected to mechanosensitive ion channels. When a sound causes the stereocilia to move, mechanosensitive ion channels transduce the signal to the cochlear nerve.

Sensory receptors for different senses are very different from each other, and they are specialized according to the type of stimulus they sense: they

have receptor specificity. For example, touch receptors, light receptors, and sound receptors are each activated by different stimuli. Touch receptors are not sensitive to light or sound; they are sensitive only to touch or pressure. However, stimuli may be combined at higher levels in the brain, as happens with olfaction, contributing to our sense of taste.

Encoding and Transmission of Sensory Information

Four aspects of sensory information are encoded by sensory systems: the type of stimulus, the location of the stimulus in the receptive field, the duration of the stimulus, and the relative intensity of the stimulus. Thus, action potentials transmitted over a sensory receptor's afferent axons encode one type of stimulus, and this segregation of the senses is preserved in other sensory circuits. For example, auditory receptors transmit signals over their own dedicated system, and electrical activity in the axons of the auditory receptors will be interpreted by the brain as an auditory stimulus— a sound.

The intensity of a stimulus is often encoded in the rate of action potentials produced by the sensory receptor. Thus, an intense stimulus will produce a more rapid train of action potentials, and reducing the stimulus will likewise slow the rate of production of action potentials. A second way in which intensity is encoded is by the number of receptors activated. An intense stimulus might initiate action potentials in a large number of adjacent receptors, while a less intense stimulus might stimulate fewer receptors. Integration of sensory information begins as soon as the information is received in the CNS, and the brain will further process incoming signals.

Perception

Perception is an individual's interpretation of a sensation. Although perception relies on the activation of sensory receptors, perception happens not at the level of the sensory receptor, but at higher levels in the nervous system, in the brain. The brain distinguishes sensory stimuli through a

sensory pathway: action potentials from sensory receptors travel along neurons that are dedicated to a particular stimulus. These neurons are dedicated to that particular stimulus and synapse with particular neurons in the brain or spinal cord.

All sensory signals, except those from the olfactory system, are transmitted though the central nervous system and are routed to the thalamus and to the appropriate region of the cortex. Recall that the thalamus is a structure in the forebrain that serves as a clearinghouse and relay station for sensory (as well as motor) signals. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex ([link]) dedicated to processing that particular sense.

How are neural signals interpreted? Interpretation of sensory signals between individuals of the same species is largely similar, owing to the inherited similarity of their nervous systems; however, there are some individual differences. A good example of this is individual tolerances to a painful stimulus, such as dental pain, which certainly differ.
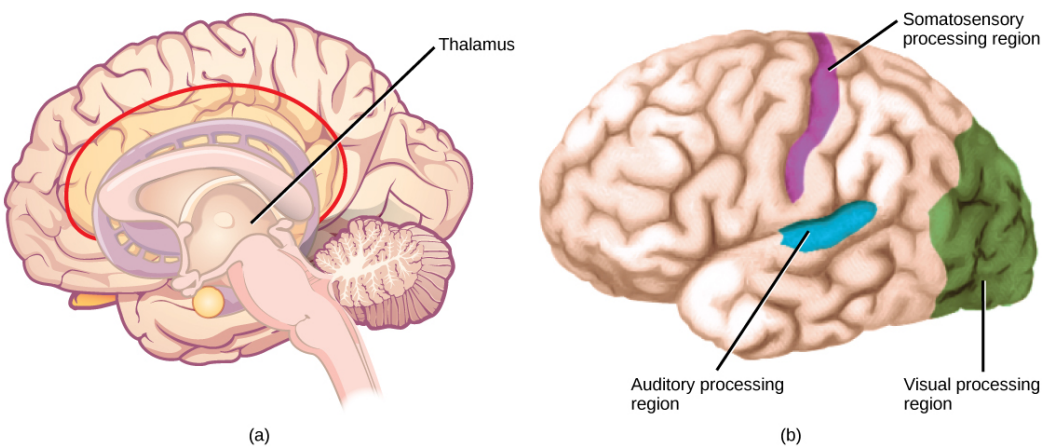
In humans, with the exception of olfaction, all sensory signals are routed from the (a) thalamus to (b) final processing regions in the cortex of the brain. (credit b: modification of work by Polina Tishina)

Scientific Method Connection

Just-Noticeable Difference

It is easy to differentiate between a one-pound bag of rice and a two-pound bag of rice. There is a one-pound difference, and one bag is twice as heavy as the other. However, would it be as easy to differentiate between a 20- and a 21-pound bag?

Question: What is the smallest detectible weight difference between a one-pound bag of rice and a larger bag? What is the smallest detectible difference between a 20-pound bag and a larger bag? In both cases, at what weights are the differences detected? This smallest detectible difference in stimuli is known as the just-noticeable difference (JND).

Background: Research background literature on JND and on Weber's Law, a description of a proposed mathematical relationship between the overall magnitude of the stimulus and the JND. You will be testing JND of different weights of rice in bags. Choose a convenient increment that is to be stepped through while testing. For example, you could choose 10 percent increments between one and two pounds (1.1, 1.2, 1.3, 1.4, and so on) or 20 percent increments (1.2, 1.4, 1.6, and 1.8).

Hypothesis: Develop a hypothesis about JND in terms of percentage of the whole weight being tested (such as "the JND between the two small bags and between the two large bags is proportionally the same," or ". . . is not proportionally the same.") So, for the first hypothesis, if the JND between the one-pound bag and a larger bag is 0.2 pounds (that is, 20 percent; 1.0 pound feels the same as 1.1 pounds, but 1.0 pound feels less than 1.2 pounds), then the JND between the 20-pound bag and a larger bag will also be 20 percent. (So, 20 pounds feels the same as 22 pounds or 23 pounds, but 20 pounds feels less than 24 pounds.)

Test the hypothesis: Enlist 24 participants, and split them into two groups of 12. To set up the demonstration, assuming a 10 percent increment was selected, have the first group be the one-pound group. As a counter-balancing measure against a systematic error, however, six of the first group will compare one pound to two pounds, and step down in weight (1.0 to 2.0, 1.0 to 1.9, and so on.), while the other six will step up (1.0 to 1.1, 1.0 to 1.2, and so on). Apply the same principle to the 20-pound group (20 to 40, 20 to 38, and so on, and 20 to 22, 20 to 24, and so on). Given the large difference between 20 and 40 pounds, you may wish to use 30

pounds as your larger weight. In any case, use two weights that are easily detectable as different.

Record the observations: Record the data in a table similar to the table below. For the one-pound and 20-pound groups (base weights) record a plus sign (+) for each participant that detects a difference between the base weight and the step weight. Record a minus sign (-) for each participant that finds no difference. If one-tenth steps were not used, then replace the steps in the "Step Weight" columns with the step you are using.

Results of JND Testing (+ = difference; – = no difference)			
Step Weight	**One pound**	**20 pounds**	**Step Weight**
1.1			22
1.2			24
1.3			26
1.4			28
1.5			30
1.6			32
1.7			34
1.8			36
1.9			38
2.0			40

Analyze the data/report the results: What step weight did all participants find to be equal with one-pound base weight? What about the 20-pound group?

Draw a conclusion: Did the data support the hypothesis? Are the final weights proportionally the same? If not, why not? Do the findings adhere to Weber's Law? Weber's Law states that the concept that a just-noticeable difference in a stimulus is proportional to the magnitude of the original stimulus.

Section Summary

A sensory activation occurs when a physical or chemical stimulus is processed into a neural signal (sensory transduction) by a sensory receptor. Perception is an individual interpretation of a sensation and is a brain function. Humans have special senses: olfaction, gustation, equilibrium, and hearing, plus the general senses of somatosensation.

Sensory receptors are either specialized cells associated with sensory neurons or the specialized ends of sensory neurons that are a part of the peripheral nervous system, and they are used to receive information about the environment (internal or external). Each sensory receptor is modified for the type of stimulus it detects. For example, neither gustatory receptors nor auditory receptors are sensitive to light. Each sensory receptor is responsive to stimuli within a specific region in space, which is known as that receptor's receptive field. The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system.

All sensory signals, except those from the olfactory system, enter the central nervous system and are routed to the thalamus. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex dedicated to processing that particular sense.

Review Questions

Exercise:

Problem: Where does perception occur?

   a. spinal cord
   b. cerebral cortex
   c. receptors
   d. thalamus

Solution:

B

Exercise:

Problem:

If a person's cold receptors no longer convert cold stimuli into sensory signals, that person has a problem with the process of _____.

   a. reception
   b. transmission
   c. perception
   d. transduction

Solution:

D

Exercise:

Problem:

After somatosensory transduction, the sensory signal travels through the brain as a(n) _____ signal.

   a. electrical
   b. pressure

c. optical

d. thermal

Solution:

A

Free Response

Exercise:

Problem:

If a person sustains damage to axons leading from sensory receptors to the central nervous system, which step or steps of sensory perception will be affected?

Solution:

Transmission of sensory information from the receptor to the central nervous system will be impaired, and thus, perception of stimuli, which occurs in the brain, will be halted.

Exercise:

Problem:

In what way does the overall magnitude of a stimulus affect the just-noticeable difference in the perception of that stimulus?

Solution:

The just-noticeable difference is a fraction of the overall magnitude of the stimulus and seems to be a relatively fixed proportion (such as 10 percent) whether the stimulus is large (such as a very heavy object) or small (such as a very light object).

Glossary

kinesthesia
    sense of body movement

mechanoreceptor
    sensory receptor modified to respond to mechanical disturbance such
    as being bent, touch, pressure, motion, and sound

perception
    individual interpretation of a sensation; a brain function

proprioception
    sense of limb position; used to track kinesthesia

reception
    receipt of a signal (such as light or sound) by sensory receptors

receptive field
    region in space in which a stimulus can activate a given sensory
    receptor

receptor potential
    membrane potential in a sensory receptor in response to detection of a
    stimulus

sensory receptor
    specialized neuron or other cells associated with a neuron that is
    modified to receive specific sensory input

sensory transduction
    conversion of a sensory stimulus into electrical energy in the nervous
    system by a change in the membrane potential

vestibular sense
    sense of spatial orientation and balance

Somatosensation

By the end of this section, you will be able to:

- Describe four important mechanoreceptors in human skin
- Describe the topographical distribution of somatosensory receptors between glabrous and hairy skin
- Explain why the perception of pain is subjective

Somatosensation is a mixed sensory category and includes all sensation received from the skin and mucous membranes, as well from as the limbs and joints. Somatosensation is also known as tactile sense, or more familiarly, as the sense of touch. Somatosensation occurs all over the exterior of the body and at some interior locations as well. A variety of receptor types—embedded in the skin, mucous membranes, muscles, joints, internal organs, and cardiovascular system—play a role.

Recall that the epidermis is the outermost layer of skin in mammals. It is relatively thin, is composed of keratin-filled cells, and has no blood supply. The epidermis serves as a barrier to water and to invasion by pathogens. Below this, the much thicker dermis contains blood vessels, sweat glands, hair follicles, lymph vessels, and lipid-secreting sebaceous glands ([link]). Below the epidermis and dermis is the subcutaneous tissue, or hypodermis, the fatty layer that contains blood vessels, connective tissue, and the axons of sensory neurons. The hypodermis, which holds about 50 percent of the body's fat, attaches the dermis to the bone and muscle, and supplies nerves and blood vessels to the dermis.
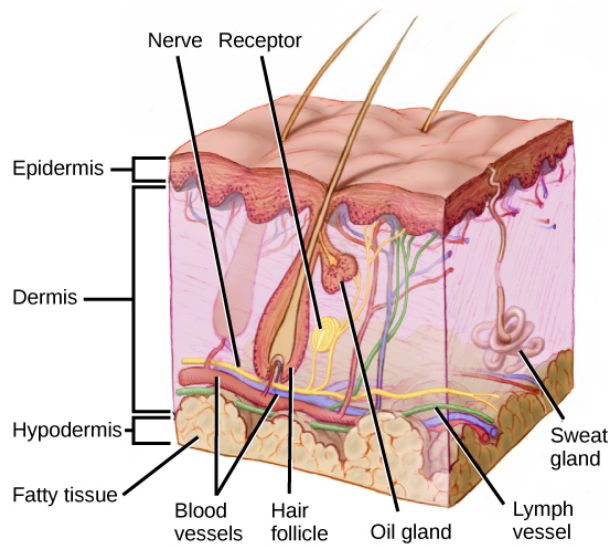
Mammalian skin has three layers: an epidermis, a dermis, and a hypodermis. (credit: modification of work by Don Bliss, National Cancer Institute)

Somatosensory Receptors

Sensory receptors are classified into five categories: mechanoreceptors, thermoreceptors, proprioceptors, pain receptors, and chemoreceptors. These categories are based on the nature of stimuli each receptor class transduces. What is commonly referred to as "touch" involves more than one kind of stimulus and more than one kind of receptor. Mechanoreceptors in the skin are described as encapsulated (that is, surrounded by a capsule) or unencapsulated (a group that includes free nerve endings). A **free nerve ending**, as its name implies, is an unencapsulated dendrite of a sensory neuron. Free nerve endings are the most common nerve endings in skin, and they extend into the middle of the epidermis. Free nerve endings are sensitive to painful stimuli, to hot and cold, and to light touch. They are slow to adjust to a stimulus and so are less sensitive to abrupt changes in stimulation.

There are three classes of mechanoreceptors: tactile, proprioceptors, and baroreceptors. Mechanoreceptors sense stimuli due to physical deformation of their plasma membranes. They contain mechanically gated ion channels whose gates open or close in response to pressure, touch, stretching, and sound." There are four primary tactile mechanoreceptors in human skin: Merkel's disks, Meissner's corpuscles, Ruffini endings, and Pacinian corpuscle; two are located toward the surface of the skin and two are located deeper. A fifth type of mechanoreceptor, Krause end bulbs, are found only in specialized regions. **Merkel's disks** (shown in [link]) are found in the upper layers of skin near the base of the epidermis, both in skin that has hair and on **glabrous** skin, that is, the hairless skin found on the palms and fingers, the soles of the feet, and the lips of humans and other primates. Merkel's disks are densely distributed in the fingertips and lips. They are slow-adapting, encapsulated nerve endings, and they respond to light touch. Light touch, also known as discriminative touch, is a light pressure that allows the location of a stimulus to be pinpointed. The receptive fields of Merkel's disks are small with well-defined borders. That makes them finely sensitive to edges and they come into use in tasks such as typing on a keyboard.

Note:
Art Connection
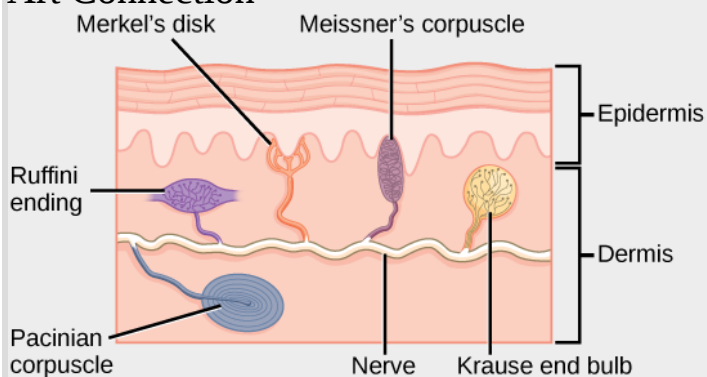
Four of the primary mechanoreceptors in human skin are shown. Merkel's disks, which are unencapsulated, respond to light touch. Meissner's

corpuscles, Ruffini endings, Pacinian corpuscles, and Krause end bulbs are all encapsulated. Meissner's corpuscles respond to touch and low-frequency vibration. Ruffini endings detect stretch, deformation within joints, and warmth. Pacinian corpuscles detect transient pressure and high-frequency vibration. Krause end bulbs detect cold.

Which of the following statements about mechanoreceptors is false?

a. Pacini corpuscles are found in both glabrous and hairy skin.
b. Merkel's disks are abundant on the fingertips and lips.
c. Ruffini endings are encapsulated mechanoreceptors.
d. Meissner's corpuscles extend into the lower dermis.

Meissner's corpuscles, (shown in [link]) also known as tactile corpuscles, are found in the upper dermis, but they project into the epidermis. They, too, are found primarily in the glabrous skin on the fingertips and eyelids. They respond to fine touch and pressure, but they also respond to low-frequency vibration or flutter. They are rapidly adapting, fluid-filled, encapsulated neurons with small, well-defined borders and are responsive to fine details. Like Merkel's disks, Meissner's corpuscles are not as plentiful in the palms as they are in the fingertips.
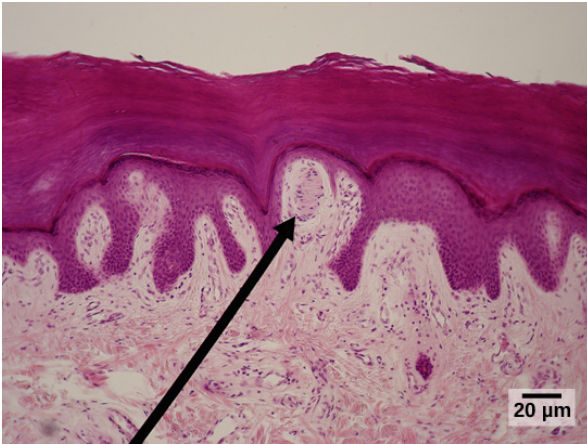
Meissner corpuscles in the fingertips, such as the one viewed here using bright field light microscopy, allow for touch discrimination of fine detail. (credit: modification of work by "Wbensmith"/Wikimedia Commons; scale-bar data from Matt Russell)

Deeper in the epidermis, near the base, are **Ruffini endings**, which are also known as bulbous corpuscles. They are found in both glabrous and hairy skin. These are slow-adapting, encapsulated mechanoreceptors that detect skin stretch and deformations within joints, so they provide valuable feedback for gripping objects and controlling finger position and movement. Thus, they also contribute to proprioception and kinesthesia. Ruffini endings also detect warmth. Note that these warmth detectors are situated deeper in the skin than are the cold detectors. It is not surprising, then, that humans detect cold stimuli before they detect warm stimuli.

Pacinian corpuscles (seen in [link]) are located deep in the dermis of both glabrous and hairy skin and are structurally similar to Meissner's corpuscles; they are found in the bone periosteum, joint capsules, pancreas

and other viscera, breast, and genitals. They are rapidly adapting mechanoreceptors that sense deep transient (but not prolonged) pressure and high-frequency vibration. Pacinian receptors detect pressure and vibration by being compressed, stimulating their internal dendrites. There are fewer Pacinian corpuscles and Ruffini endings in skin than there are Merkel's disks and Meissner's corpuscles.
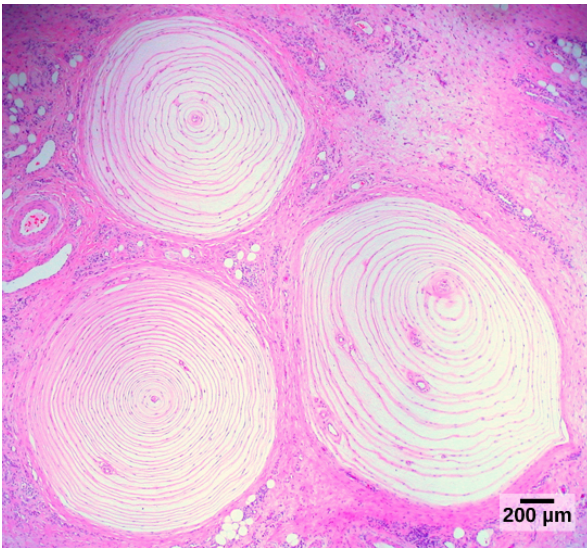
Pacinian corpuscles, such as these visualized using bright field light microscopy, detect pressure (touch) and high-frequency vibration. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

In proprioception, proprioceptive and kinesthetic signals travel through myelinated afferent neurons running from the spinal cord to the medulla. Neurons are not physically connected, but communicate via neurotransmitters secreted into synapses or "gaps" between communicating

neurons. Once in the medulla, the neurons continue carrying the signals to the thalamus.

Muscle spindles are stretch receptors that detect the amount of stretch, or lengthening of muscles. Related to these are **Golgi tendon organs**, which are tension receptors that detect the force of muscle contraction. Proprioceptive and kinesthetic signals come from limbs. Unconscious proprioceptive signals run from the spinal cord to the cerebellum, the brain region that coordinates muscle contraction, rather than to the thalamus, like most other sensory information.

Barorecptors detect pressure changes in an organ. They are found in the walls of the carotid artery and the aorta where they monitor blood pressure, and in the lungs where they detect the degree of lung expansion. Stretch receptors are found at various sites in the digestive and urinary systems.

In addition to these two types of deeper receptors, there are also rapidly adapting hair receptors, which are found on nerve endings that wrap around the base of hair follicles. There are a few types of hair receptors that detect slow and rapid hair movement, and they differ in their sensitivity to movement. Some hair receptors also detect skin deflection, and certain rapidly adapting hair receptors allow detection of stimuli that have not yet touched the skin.

Integration of Signals from Mechanoreceptors

The configuration of the different types of receptors working in concert in human skin results in a very refined sense of touch. The nociceptive receptors—those that detect pain—are located near the surface. Small, finely calibrated mechanoreceptors—Merkel's disks and Meissner's corpuscles—are located in the upper layers and can precisely localize even gentle touch. The large mechanoreceptors—Pacinian corpuscles and Ruffini endings—are located in the lower layers and respond to deeper touch. (Consider that the deep pressure that reaches those deeper receptors would not need to be finely localized.) Both the upper and lower layers of the skin hold rapidly and slowly adapting receptors. Both primary somatosensory

cortex and secondary cortical areas are responsible for processing the complex picture of stimuli transmitted from the interplay of mechanoreceptors.

Density of Mechanoreceptors

The distribution of touch receptors in human skin is not consistent over the body. In humans, touch receptors are less dense in skin covered with any type of hair, such as the arms, legs, torso, and face. Touch receptors are denser in glabrous skin (the type found on human fingertips and lips, for example), which is typically more sensitive and is thicker than hairy skin (4 to 5 mm versus 2 to 3 mm).

How is receptor density estimated in a human subject? The relative density of pressure receptors in different locations on the body can be demonstrated experimentally using a two-point discrimination test. In this demonstration, two sharp points, such as two thumbtacks, are brought into contact with the subject's skin (though not hard enough to cause pain or break the skin). The subject reports if he or she feels one point or two points. If the two points are felt as one point, it can be inferred that the two points are both in the receptive field of a single sensory receptor. If two points are felt as two separate points, each is in the receptive field of two separate sensory receptors. The points could then be moved closer and re-tested until the subject reports feeling only one point, and the size of the receptive field of a single receptor could be estimated from that distance.

Thermoreception

In addition to Krause end bulbs that detect cold and Ruffini endings that detect warmth, there are different types of cold receptors on some free nerve endings: thermoreceptors, located in the dermis, skeletal muscles, liver, and hypothalamus, that are activated by different temperatures. Their pathways into the brain run from the spinal cord through the thalamus to the primary somatosensory cortex. Warmth and cold information from the face travels through one of the cranial nerves to the brain. You know from

experience that a tolerably cold or hot stimulus can quickly progress to a much more intense stimulus that is no longer tolerable. Any stimulus that is too intense can be perceived as pain because temperature sensations are conducted along the same pathways that carry pain sensations

Pain

Pain is the name given to **nociception**, which is the neural processing of injurious stimuli in response to tissue damage. Pain is caused by true sources of injury, such as contact with a heat source that causes a thermal burn or contact with a corrosive chemical. But pain also can be caused by harmless stimuli that mimic the action of damaging stimuli, such as contact with capsaicins, the compounds that cause peppers to taste hot and which are used in self-defense pepper sprays and certain topical medications. Peppers taste "hot" because the protein receptors that bind capsaicin open the same calcium channels that are activated by warm receptors.

Nociception starts at the sensory receptors, but pain, inasmuch as it is the perception of nociception, does not start until it is communicated to the brain. There are several nociceptive pathways to and through the brain. Most axons carrying nociceptive information into the brain from the spinal cord project to the thalamus (as do other sensory neurons) and the neural signal undergoes final processing in the primary somatosensory cortex. Interestingly, one nociceptive pathway projects not to the thalamus but directly to the hypothalamus in the forebrain, which modulates the cardiovascular and neuroendocrine functions of the autonomic nervous system. Recall that threatening—or painful—stimuli stimulate the sympathetic branch of the visceral sensory system, readying a fight-or-flight response.

Note:
Link to Learning

View this [video](https://www.openstaxcollege.org/l/nociceptive) that animates the five phases of nociceptive pain. https://www.openstaxcollege.org/l/nociceptive

Section Summary

Somatosensation includes all sensation received from the skin and mucous membranes, as well as from the limbs and joints. Somatosensation occurs all over the exterior of the body and at some interior locations as well, and a variety of receptor types, embedded in the skin and mucous membranes, play a role.

There are several types of specialized sensory receptors. Rapidly adapting free nerve endings detect nociception, hot and cold, and light touch. Slowly adapting, encapsulated Merkel's disks are found in fingertips and lips, and respond to light touch. Meissner's corpuscles, found in glabrous skin, are rapidly adapting, encapsulated receptors that detect touch, low-frequency vibration, and flutter. Ruffini endings are slowly adapting, encapsulated receptors that detect skin stretch, joint activity, and warmth. Hair receptors are rapidly adapting nerve endings wrapped around the base of hair follicles that detect hair movement and skin deflection. Finally, Pacinian corpuscles are encapsulated, rapidly adapting receptors that detect transient pressure and high-frequency vibration.

Art Connections

Exercise:

Problem:

[link] Which of the following statements about mechanoreceptors is false?

    a. Pacini corpuscles are found in both glabrous and hairy skin.
    b. Merkel's disks are abundant on the fingertips and lips.
    c. Ruffini endings are encapsulated mechanoreceptors.
    d. Meissner's corpuscles extend into the lower dermis.

Solution:

[link] D

Review Questions

Exercise:

Problem:

_____ are found only in _____ skin, and detect skin deflection.

    a. Meissner's corpuscles: hairy
    b. Merkel's disks: glabrous
    c. hair receptors: hairy
    d. Krause end bulbs: hairy

Solution:

B

Exercise:

Problem:

If you were to burn your epidermis, what receptor type would you most likely burn?

a. free nerve endings
b. Ruffini endings
c. Pacinian corpuscle
d. hair receptors

Solution:

A

Free Response

Exercise:

Problem:

What can be inferred about the relative sizes of the areas of cortex that process signals from skin not densely innervated with sensory receptors and skin that is densely innervated with sensory receptors?

Solution:

The cortical areas serving skin that is densely innervated likely are larger than those serving skin that is less densely innervated.

Glossary

free nerve ending
    ending of an afferent neuron that lacks a specialized structure for detection of sensory stimuli; some respond to touch, pain, or temperature

glabrous
    describes the non-hairy skin found on palms and fingers, soles of feet, and lips of humans and other primates

Golgi tendon organ

muscular proprioceptive tension receptor that provides the sensory
component of the Golgi tendon reflex

Meissner's corpuscle
(also, tactile corpuscle) encapsulated, rapidly-adapting
mechanoreceptor in the skin that responds to light touch

Merkel's disc
unencapsulated, slowly-adapting mechanoreceptor in the skin that
responds to touch

muscle spindle
proprioceptive stretch receptor that lies within a muscle and that
shortens the muscle to an optimal length for efficient contraction

nociception
neural processing of noxious (such as damaging) stimuli

Pacinian corpuscle
encapsulated mechanoreceptor in the skin that responds to deep
pressure and vibration

Ruffini ending
(also, bulbous corpuscle) slowly-adapting mechanoreceptor in the skin
that responds to skin stretch and joint position

Taste and Smell
By the end of this section, you will be able to:

- Explain in what way smell and taste stimuli differ from other sensory stimuli
- Identify the five primary tastes that can be distinguished by humans
- Explain in anatomical terms why a dog's sense of smell is more acute than a human's

Taste, also called **gustation**, and smell, also called **olfaction**, are the most interconnected senses in that both involve molecules of the stimulus entering the body and bonding to receptors. Smell lets an animal sense the presence of food or other animals—whether potential mates, predators, or prey—or other chemicals in the environment that can impact their survival. Similarly, the sense of taste allows animals to discriminate between types of foods. While the value of a sense of smell is obvious, what is the value of a sense of taste? Different tasting foods have different attributes, both helpful and harmful. For example, sweet-tasting substances tend to be highly caloric, which could be necessary for survival in lean times. Bitterness is associated with toxicity, and sourness is associated with spoiled food. Salty foods are valuable in maintaining homeostasis by helping the body retain water and by providing ions necessary for cells to function.

Tastes and Odors

Both taste and odor stimuli are molecules taken in from the environment. The primary tastes detected by humans are sweet, sour, bitter, salty and umami. The first four tastes need little explanation. The identification of **umami** as a fundamental taste occurred fairly recently—it was identified in 1908 by Japanese scientist Kikunae Ikeda while he worked with seaweed broth, but it was not widely accepted as a taste that could be physiologically distinguished until many years later. The taste of umami, also known as savoriness, is attributable to the taste of the amino acid L-glutamate. In fact, monosodium glutamate, or MSG, is often used in cooking to enhance the savory taste of certain foods. What is the adaptive value of being able to distinguish umami? Savory substances tend to be high in protein.

All odors that we perceive are molecules in the air we breathe. If a substance does not release molecules into the air from its surface, it has no smell. And if a human or other animal does not have a receptor that recognizes a specific molecule, then that molecule has no smell. Humans have about 350 olfactory receptor subtypes that work in various combinations to allow us to sense about 10,000 different odors. Compare that to mice, for example, which have about 1,300 olfactory receptor types, and therefore probably sense more odors. Both odors and tastes involve molecules that stimulate specific chemoreceptors. Although humans commonly distinguish taste as one sense and smell as another, they work together to create the perception of flavor. A person's perception of flavor is reduced if he or she has congested nasal passages.

Reception and Transduction

Odorants (odor molecules) enter the nose and dissolve in the olfactory epithelium, the mucosa at the back of the nasal cavity (as illustrated in [link]). The **olfactory epithelium** is a collection of specialized olfactory receptors in the back of the nasal cavity that spans an area about 5 cm^2 in humans. Recall that sensory cells are neurons. An **olfactory receptor**, which is a dendrite of a specialized neuron, responds when it binds certain molecules inhaled from the environment by sending impulses directly to the olfactory bulb of the brain. Humans have about 12 million olfactory receptors, distributed among hundreds of different receptor types that respond to different odors. Twelve million seems like a large number of receptors, but compare that to other animals: rabbits have about 100 million, most dogs have about 1 billion, and bloodhounds—dogs selectively bred for their sense of smell—have about 4 billion. The overall size of the olfactory epithelium also differs between species, with that of bloodhounds, for example, being many times larger than that of humans.

Olfactory neurons are **bipolar neurons** (neurons with two processes from the cell body). Each neuron has a single dendrite buried in the olfactory epithelium, and extending from this dendrite are 5 to 20 receptor-laden, hair-like cilia that trap odorant molecules. The sensory receptors on the cilia are proteins, and it is the variations in their amino acid chains that make the receptors sensitive to different odorants. Each olfactory sensory neuron has

only one type of receptor on its cilia, and the receptors are specialized to detect specific odorants, so the bipolar neurons themselves are specialized. When an odorant binds with a receptor that recognizes it, the sensory neuron associated with the receptor is stimulated. Olfactory stimulation is the only sensory information that directly reaches the cerebral cortex, whereas other sensations are relayed through the thalamus.
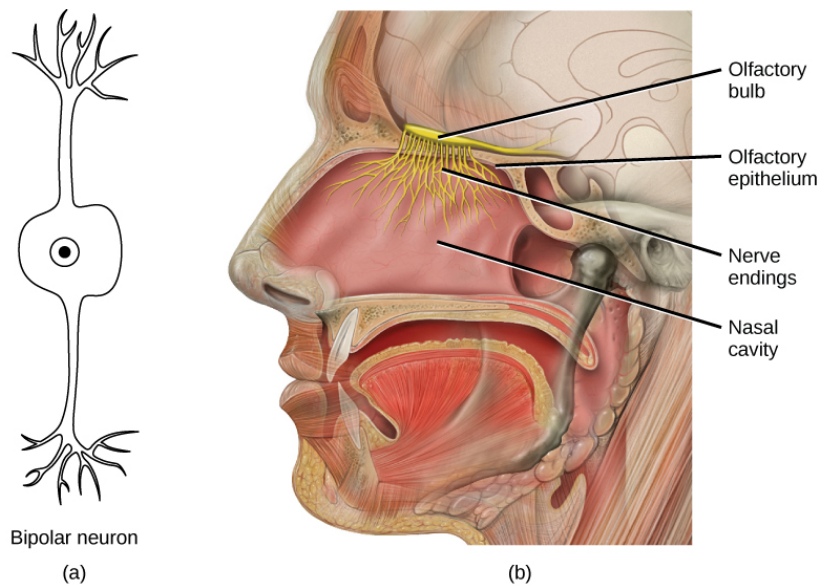
Bipolar neuron
(a)   (b)

In the human olfactory system, (a) bipolar olfactory neurons extend from (b) the olfactory epithelium, where olfactory receptors are located, to the olfactory bulb. (credit: modification of work by Patrick J. Lynch, medical illustrator; C. Carl Jaffe, MD, cardiologist)

Note:
Evolution Connection
Pheromones

A **pheromone** is a chemical released by an animal that affects the behavior or physiology of animals of the same species. Pheromonal signals can have profound effects on animals that inhale them, but pheromones apparently are not consciously perceived in the same way as other odors. There are several different types of pheromones, which are released in urine or as glandular secretions. Certain pheromones are attractants to potential mates, others are repellants to potential competitors of the same sex, and still others play roles in mother-infant attachment. Some pheromones can also influence the timing of puberty, modify reproductive cycles, and even prevent embryonic implantation. While the roles of pheromones in many nonhuman species are important, pheromones have become less important in human behavior over evolutionary time compared to their importance to organisms with more limited behavioral repertoires.

The vomeronasal organ (VNO, or Jacobson's organ) is a tubular, fluid-filled, olfactory organ present in many vertebrate animals that sits adjacent to the nasal cavity. It is very sensitive to pheromones and is connected to the nasal cavity by a duct. When molecules dissolve in the mucosa of the nasal cavity, they then enter the VNO where the pheromone molecules among them bind with specialized pheromone receptors. Upon exposure to pheromones from their own species or others, many animals, including cats, may display the flehmen response (shown in [link]), a curling of the upper lip that helps pheromone molecules enter the VNO.

Pheromonal signals are sent, not to the main olfactory bulb, but to a different neural structure that projects directly to the amygdala (recall that the amygdala is a brain center important in emotional reactions, such as fear). The pheromonal signal then continues to areas of the hypothalamus that are key to reproductive physiology and behavior. While some scientists assert that the VNO is apparently functionally vestigial in humans, even though there is a similar structure located near human nasal cavities, others are researching it as a possible functional system that may, for example, contribute to synchronization of menstrual cycles in women living in close proximity.

The flehmen response in this tiger results in the curling of the upper lip and helps airborne pheromone molecules enter the vomeronasal organ. (credit: modification of work by "chadh"/Flickr)

Taste

Detecting a taste (gustation) is fairly similar to detecting an odor (olfaction), given that both taste and smell rely on chemical receptors being stimulated by certain molecules. The primary organ of taste is the taste bud. A **taste bud** is a cluster of gustatory receptors (taste cells) that are located within the bumps on the tongue called **papillae** (singular: papilla) (illustrated in [link]). There are several structurally distinct papillae. Filiform papillae, which are located across the tongue, are tactile, providing friction that helps the tongue move substances, and contain no taste cells. In contrast, fungiform papillae, which are located mainly on the anterior two-thirds of the tongue, each contain one to eight taste buds and also have receptors for pressure and temperature. The large circumvallate papillae contain up to 100 taste buds and form a V near the posterior margin of the tongue.
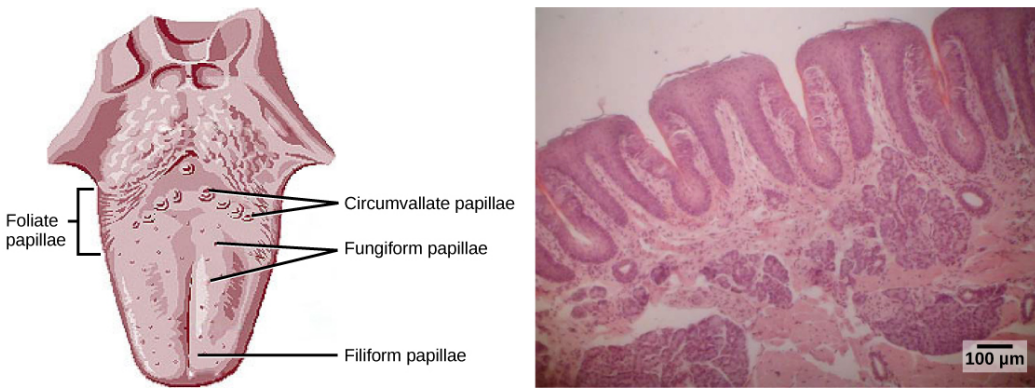
(a) Foliate, circumvallate, and fungiform papillae are located on different regions of the tongue. (b) Foliate papillae are prominent protrusions on this light micrograph. (credit a: modification of work by NCI; scale-bar data from Matt Russell)

In addition to those two types of chemically and mechanically sensitive papillae are foliate papillae—leaf-like papillae located in parallel folds along the edges and toward the back of the tongue, as seen in the [link] micrograph. Foliate papillae contain about 1,300 taste buds within their folds. Finally, there are circumvallate papillae, which are wall-like papillae in the shape of an inverted "V" at the back of the tongue. Each of these papillae is surrounded by a groove and contains about 250 taste buds.

Each taste bud's taste cells are replaced every 10 to 14 days. These are elongated cells with hair-like processes called microvilli at the tips that extend into the taste bud pore (illustrate in [link]). Food molecules (**tastants**) are dissolved in saliva, and they bind with and stimulate the receptors on the microvilli. The receptors for tastants are located across the outer portion and front of the tongue, outside of the middle area where the filiform papillae are most prominent.
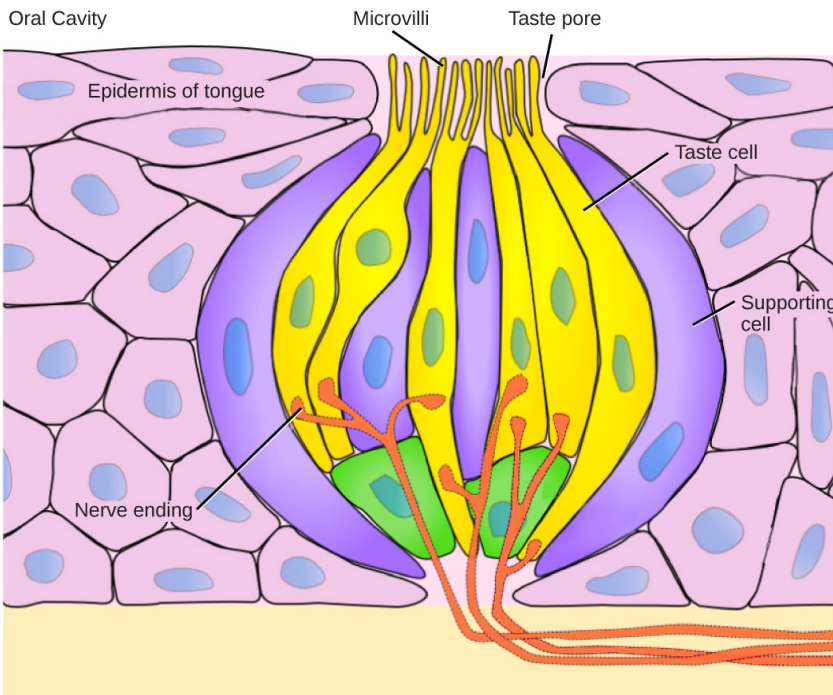
Pores in the tongue allow tastants to enter taste pores in the tongue. (credit: modification of work by Vincenzo Rizzo)

In humans, there are five primary tastes, and each taste has only one corresponding type of receptor. Thus, like olfaction, each receptor is specific to its stimulus (tastant). Transduction of the five tastes happens through different mechanisms that reflect the molecular composition of the tastant. A salty tastant (containing NaCl) provides the sodium ions (Na^+) that enter the taste neurons and excite them directly. Sour tastants are acids and belong to the thermoreceptor protein family. Binding of an acid or other sour-tasting molecule triggers a change in the ion channel and these increase hydrogen ion (H^+) concentrations in the taste neurons, thus depolarizing them. Sweet, bitter, and umami tastants require a G-protein coupled receptor. These tastants bind to their respective receptors, thereby exciting the specialized neurons associated with them.

Both tasting abilities and sense of smell change with age. In humans, the senses decline dramatically by age 50 and continue to decline. A child may

find a food to be too spicy, whereas an elderly person may find the same food to be bland and unappetizing.

Smell and Taste in the Brain

Olfactory neurons project from the olfactory epithelium to the olfactory bulb as thin, unmyelinated axons. The **olfactory bulb** is composed of neural clusters called **glomeruli**, and each glomerulus receives signals from one type of olfactory receptor, so each glomerulus is specific to one odorant. From glomeruli, olfactory signals travel directly to the olfactory cortex and then to the frontal cortex and the thalamus. Recall that this is a different path from most other sensory information, which is sent directly to the thalamus before ending up in the cortex. Olfactory signals also travel directly to the amygdala, thereafter reaching the hypothalamus, thalamus, and frontal cortex. The last structure that olfactory signals directly travel to is a cortical center in the temporal lobe structure important in spatial, autobiographical, declarative, and episodic memories. Olfaction is finally processed by areas of the brain that deal with memory, emotions, reproduction, and thought.

Taste neurons project from taste cells in the tongue, esophagus, and palate to the medulla, in the brainstem. From the medulla, taste signals travel to the thalamus and then to the primary gustatory cortex. Information from

different regions of the tongue is segregated in the medulla, thalamus, and cortex.

Section Summary

There are five primary tastes in humans: sweet, sour, bitter, salty, and umami. Each taste has its own receptor type that responds only to that taste. Tastants enter the body and are dissolved in saliva. Taste cells are located within taste buds, which are found on three of the four types of papillae in the mouth.

Regarding olfaction, there are many thousands of odorants, but humans detect only about 10,000. Like taste receptors, olfactory receptors are each responsive to only one odorant. Odorants dissolve in nasal mucosa, where they excite their corresponding olfactory sensory cells. When these cells detect an odorant, they send their signals to the main olfactory bulb and then to other locations in the brain, including the olfactory cortex.

Review Questions

Exercise:

Problem: Which of the following has the fewest taste receptors?

a. fungiform papillae
b. circumvallate papillae
c. foliate papillae
d. filiform papillae

Solution:

D

Exercise:

Problem:

How many different taste molecules do taste cells each detect?

    a. one
    b. five
    c. ten
    d. It depends on the spot on the tongue

Solution:

A

Exercise:

Problem: Salty foods activate the taste cells by _____.

    a. exciting the taste cell directly
    b. causing hydrogen ions to enter the cell
    c. causing sodium channels to close
    d. binding directly to the receptors

Solution:

A

Exercise:

Problem:

All sensory signals except _____ travel to the _____ in the brain before the cerebral cortex.

    a. vision; thalamus
    b. olfaction; thalamus
    c. vision; cranial nerves
    d. olfaction; cranial nerves

Solution:

B

Free Response

Exercise:

Problem:

From the perspective of the recipient of the signal, in what ways do pheromones differ from other odorants?

Solution:

Pheromones may not be consciously perceived, and pheromones can have direct physiological and behavioral effects on their recipients.

Exercise:

Problem:

What might be the effect on an animal of not being able to perceive taste?

Solution:

The animal might not be able to recognize the differences in food sources and thus might not be able to discriminate between spoiled food and safe food or between foods that contain necessary nutrients, such as proteins, and foods that do not.

Glossary

bipolar neuron
    neuron with two processes from the cell body, typically in opposite directions

glomerulus
    in the olfactory bulb, one of the two neural clusters that receives
    signals from one type of olfactory receptor

gustation
    sense of taste

odorant
    airborne molecule that stimulates an olfactory receptor

olfaction
    sense of smell

olfactory bulb
    neural structure in the vertebrate brain that receives signals from
    olfactory receptors

olfactory epithelium
    specialized tissue in the nasal cavity where olfactory receptors are
    located

olfactory receptor
    dendrite of a specialized neuron

papilla
    one of the small bump-like projections from the tongue

pheromone
    substance released by an animal that can affect the physiology or
    behavior of other animals

tastant
    food molecule that stimulates gustatory receptors

taste bud
    clusters of taste cells

umami

one of the five basic tastes, which is described as "savory" and which may be largely the taste of L-glutamate

Hearing and Vestibular Sensation
By the end of this section, you will be able to:

- Describe the relationship of amplitude and frequency of a sound wave to attributes of sound
- Trace the path of sound through the auditory system to the site of transduction of sound
- Identify the structures of the vestibular system that respond to gravity

Audition, or hearing, is important to humans and to other animals for many different interactions. It enables an organism to detect and receive information about danger, such as an approaching predator, and to participate in communal exchanges like those concerning territories or mating. On the other hand, although it is physically linked to the auditory system, the vestibular system is not involved in hearing. Instead, an animal's vestibular system detects its own movement, both linear and angular acceleration and deceleration, and balance.

Sound

Auditory stimuli are sound waves, which are mechanical, pressure waves that move through a medium, such as air or water. There are no sound waves in a vacuum since there are no air molecules to move in waves. The speed of sound waves differs, based on altitude, temperature, and medium, but at sea level and a temperature of 20º C (68º F), sound waves travel in the air at about 343 meters per second.

As is true for all waves, there are four main characteristics of a sound wave: frequency, wavelength, period, and amplitude. Frequency is the number of waves per unit of time, and in sound is heard as pitch. High-frequency (≥15.000Hz) sounds are higher-pitched (short wavelength) than low-frequency (long wavelengths; ≤100Hz) sounds. Frequency is measured in cycles per second, and for sound, the most commonly used unit is hertz (Hz), or cycles per second. Most humans can perceive sounds with frequencies between 30 and 20,000 Hz. Women are typically better at hearing high frequencies, but everyone's ability to hear high frequencies decreases with age. Dogs detect up to about 40,000 Hz; cats, 60,000 Hz;

bats, 100,000 Hz; and dolphins 150,000 Hz, and American shad (*Alosa sapidissima*), a fish, can hear 180,000 Hz. Those frequencies above the human range are called **ultrasound**.

Amplitude, or the dimension of a wave from peak to trough, in sound is heard as volume and is illustrated in [link]. The sound waves of louder sounds have greater amplitude than those of softer sounds. For sound, volume is measured in decibels (dB). The softest sound that a human can hear is the zero point. Humans speak normally at 60 decibels.
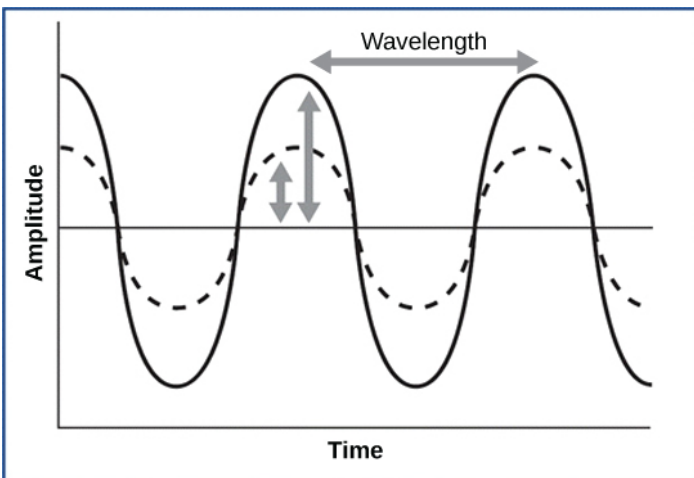
For sound waves, wavelength corresponds to pitch. Amplitude of the wave corresponds to volume. The sound wave shown with a dashed line is softer in volume than the sound wave shown with a solid line. (credit: NIH)

Reception of Sound

In mammals, sound waves are collected by the external, cartilaginous part of the ear called the **pinna**, then travel through the auditory canal and cause

vibration of the thin diaphragm called the **tympanum** or ear drum, the innermost part of the **outer ear** (illustrated in [link]). Interior to the tympanum is the **middle ear**. The middle ear holds three small bones called the **ossicles**, which transfer energy from the moving tympanum to the inner ear. The three ossicles are the **malleus** (also known as the hammer), the **incus** (the anvil), and **stapes** (the stirrup). The aptly named stapes looks very much like a stirrup. The three ossicles are unique to mammals, and each plays a role in hearing. The malleus attaches at three points to the interior surface of the tympanic membrane. The incus attaches the malleus to the stapes. In humans, the stapes is not long enough to reach the tympanum. If we did not have the malleus and the incus, then the vibrations of the tympanum would never reach the inner ear. These bones also function to collect force and amplify sounds. The ear ossicles are homologous to bones in a fish mouth: the bones that support gills in fish are thought to be adapted for use in the vertebrate ear over evolutionary time. Many animals (frogs, reptiles, and birds, for example) use the stapes of the middle ear to transmit vibrations to the middle ear.
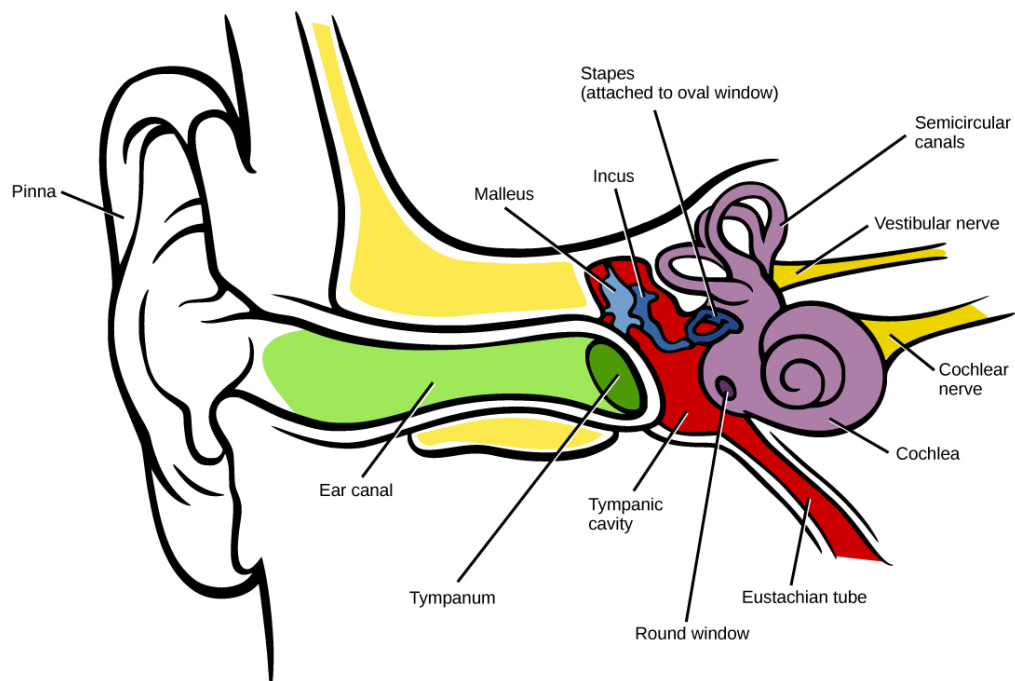
Sound travels through the outer ear to the middle ear, which is bounded on its exterior by the tympanic membrane. The

middle ear contains three bones called ossicles that transfer the sound wave to the oval window, the exterior boundary of the inner ear. The organ of Corti, which is the organ of sound transduction, lies inside the cochlea. (credit: modification of work by Lars Chittka, Axel Brockmann)

Transduction of Sound

Vibrating objects, such as vocal cords, create sound waves or pressure waves in the air. When these pressure waves reach the ear, the ear transduces this mechanical stimulus (pressure wave) into a nerve impulse (electrical signal) that the brain perceives as sound. The pressure waves strike the tympanum, causing it to vibrate. The mechanical energy from the moving tympanum transmits the vibrations to the three bones of the middle ear. The stapes transmits the vibrations to a thin diaphragm called the **oval window**, which is the outermost structure of the **inner ear**. The structures of the inner ear are found in the **labyrinth**, a bony, hollow structure that is the most interior portion of the ear. Here, the energy from the sound wave is transferred from the stapes through the flexible oval window and to the fluid of the cochlea. The vibrations of the oval window create pressure waves in the fluid (perilymph) inside the cochlea. The **cochlea** is a whorled structure, like the shell of a snail, and it contains receptors for transduction of the mechanical wave into an electrical signal (as illustrated in [link]). Inside the cochlea, the **basilar membrane** is a mechanical analyzer that runs the length of the cochlea, curling toward the cochlea's center.

The mechanical properties of the basilar membrane change along its length, such that it is thicker, tauter, and narrower at the outside of the whorl (where the cochlea is largest), and thinner, floppier, and broader toward the apex, or center, of the whorl (where the cochlea is smallest). Different regions of the basilar membrane vibrate according to the frequency of the sound wave conducted through the fluid in the cochlea. For these reasons, the fluid-filled cochlea detects different wave frequencies (pitches) at different regions of the membrane. When the sound waves in the cochlear

fluid contact the basilar membrane, it flexes back and forth in a wave-like fashion. Above the basilar membrane is the **tectorial membrane**.
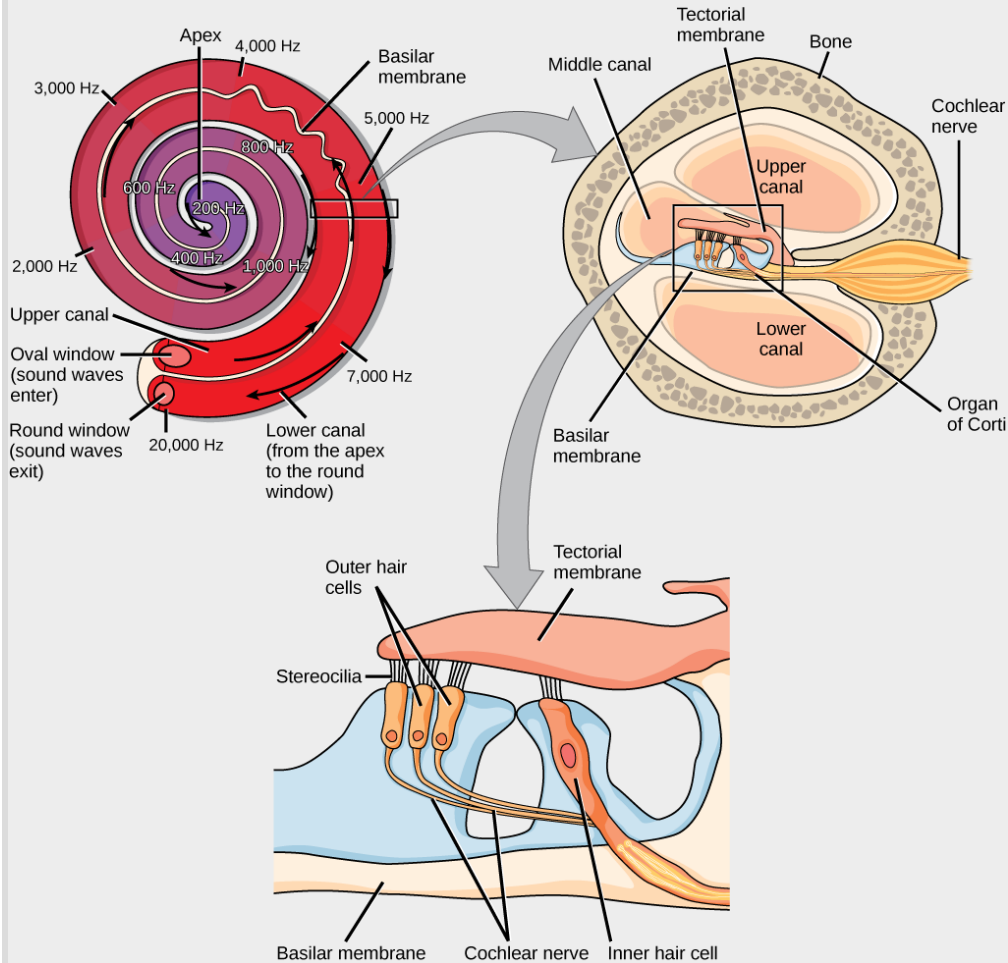
In the human ear, sound waves cause the stapes to press against the oval window. Vibrations travel up the fluid-filled interior of the cochlea. The basilar membrane that lines the cochlea gets continuously thinner toward the apex of the cochlea. Different thicknesses of membrane vibrate in response to different frequencies of sound. Sound waves then exit through the round window. In the cross section of the cochlea (top right figure), note that in

addition to the upper canal and lower canal, the cochlea also has a middle canal. The organ of Corti (bottom image) is the site of sound transduction. Movement of stereocilia on hair cells results in an action potential that travels along the auditory nerve.

Cochlear implants can restore hearing in people who have a nonfunctional cochlear. The implant consists of a microphone that picks up sound. A speech processor selects sounds in the range of human speech, and a transmitter converts these sounds to electrical impulses, which are then sent to the auditory nerve. Which of the following types of hearing loss would not be restored by a cochlear implant?

    a. Hearing loss resulting from absence or loss of hair cells in the organ of Corti.
    b. Hearing loss resulting from an abnormal auditory nerve.
    c. Hearing loss resulting from fracture of the cochlea.
    d. Hearing loss resulting from damage to bones of the middle ear.

The site of transduction is in the **organ of Corti** (spiral organ). It is composed of hair cells held in place above the basilar membrane like flowers projecting up from soil, with their exposed short, hair-like **stereocilia** contacting or embedded in the tectorial membrane above them. The inner hair cells are the primary auditory receptors and exist in a single row, numbering approximately 3,500. The stereocilia from inner hair cells extend into small dimples on the tectorial membrane's lower surface. The outer hair cells are arranged in three or four rows. They number approximately 12,000, and they function to fine tune incoming sound waves. The longer stereocilia that project from the outer hair cells actually attach to the tectorial membrane. All of the stereocilia are mechanoreceptors, and when bent by vibrations they respond by opening a gated ion channel (refer to [link]). As a result, the hair cell membrane is depolarized, and a signal is transmitted to the chochlear nerve. Intensity

(volume) of sound is determined by how many hair cells at a particular location are stimulated.

The hair cells are arranged on the basilar membrane in an orderly way. The basilar membrane vibrates in different regions, according to the frequency of the sound waves impinging on it. Likewise, the hair cells that lay above it are most sensitive to a specific frequency of sound waves. Hair cells can respond to a small range of similar frequencies, but they require stimulation of greater intensity to fire at frequencies outside of their optimal range. The difference in response frequency between adjacent inner hair cells is about 0.2 percent. Compare that to adjacent piano strings, which are about six percent different. Place theory, which is the model for how biologists think pitch detection works in the human ear, states that high frequency sounds selectively vibrate the basilar membrane of the inner ear near the entrance port (the oval window). Lower frequencies travel farther along the membrane before causing appreciable excitation of the membrane. The basic pitch-determining mechanism is based on the location along the membrane where the hair cells are stimulated. The place theory is the first step toward an understanding of pitch perception. Considering the extreme pitch sensitivity of the human ear, it is thought that there must be some auditory "sharpening" mechanism to enhance the pitch resolution.

When sound waves produce fluid waves inside the cochlea, the basilar membrane flexes, bending the stereocilia that attach to the tectorial membrane. Their bending results in action potentials in the hair cells, and auditory information travels along the neural endings of the bipolar neurons of the hair cells (collectively, the auditory nerve) to the brain. When the hairs bend, they release an excitatory neurotransmitter at a synapse with a sensory neuron, which then conducts action potentials to the central nervous system. The cochlear branch of the vestibulocochlear cranial nerve sends information on hearing. The auditory system is very refined, and there is some modulation or "sharpening" built in. The brain can send signals back to the cochlea, resulting in a change of length in the outer hair cells, sharpening or dampening the hair cells' response to certain frequencies.

Note:

Higher Processing

The inner hair cells are most important for conveying auditory information to the brain. About 90 percent of the afferent neurons carry information from inner hair cells, with each hair cell synapsing with 10 or so neurons. Outer hair cells connect to only 10 percent of the afferent neurons, and each afferent neuron innervates many hair cells. The afferent, bipolar neurons that convey auditory information travel from the cochlea to the medulla, through the pons and midbrain in the brainstem, finally reaching the primary auditory cortex in the temporal lobe.

Vestibular Information

The stimuli associated with the vestibular system are linear acceleration (gravity) and angular acceleration and deceleration. Gravity, acceleration, and deceleration are detected by evaluating the inertia on receptive cells in the vestibular system. Gravity is detected through head position. Angular acceleration and deceleration are expressed through turning or tilting of the head.

The vestibular system has some similarities with the auditory system. It utilizes hair cells just like the auditory system, but it excites them in different ways. There are five vestibular receptor organs in the inner ear: the

utricle, the saccule, and three semicircular canals. Together, they make up what's known as the vestibular labyrinth that is shown in [link]. The utricle and saccule respond to acceleration in a straight line, such as gravity. The roughly 30,000 hair cells in the utricle and 16,000 hair cells in the saccule lie below a gelatinous layer, with their stereocilia projecting into the gelatin. Embedded in this gelatin are calcium carbonate crystals—like tiny rocks. When the head is tilted, the crystals continue to be pulled straight down by gravity, but the new angle of the head causes the gelatin to shift, thereby bending the stereocilia. The bending of the stereocilia stimulates the neurons, and they signal to the brain that the head is tilted, allowing the maintenance of balance. It is the vestibular branch of the vestibulocochlear cranial nerve that deals with balance.
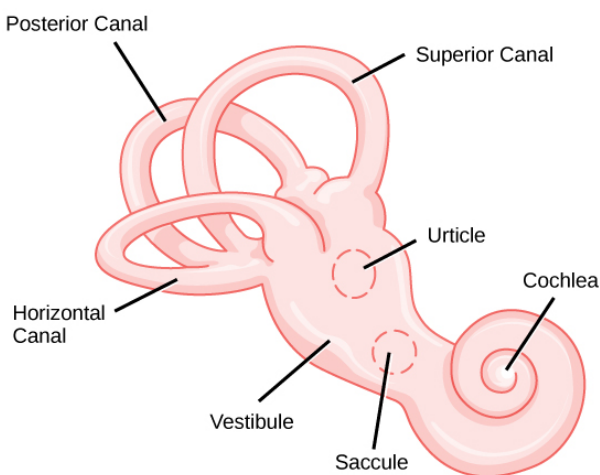
The structure of the vestibular labyrinth is shown. (credit: modification of work by NIH)

The fluid-filled **semicircular canals** are tubular loops set at oblique angles. They are arranged in three spatial planes. The base of each canal has a swelling that contains a cluster of hair cells. The hairs project into a gelatinous cap called the cupula and monitor angular acceleration and deceleration from rotation. They would be stimulated by driving your car

around a corner, turning your head, or falling forward. One canal lies horizontally, while the other two lie at about 45 degree angles to the horizontal axis, as illustrated in [link]. When the brain processes input from all three canals together, it can detect angular acceleration or deceleration in three dimensions. When the head turns, the fluid in the canals shifts, thereby bending stereocilia and sending signals to the brain. Upon cessation accelerating or decelerating—or just moving—the movement of the fluid within the canals slows or stops. For example, imagine holding a glass of water. When moving forward, water may splash backwards onto the hand, and when motion has stopped, water may splash forward onto the fingers. While in motion, the water settles in the glass and does not splash. Note that the canals are not sensitive to velocity itself, but to changes in velocity, so moving forward at 60mph with your eyes closed would not give the sensation of movement, but suddenly accelerating or braking would stimulate the receptors.

Higher Processing

Hair cells from the utricle, saccule, and semicircular canals also communicate through bipolar neurons to the cochlear nucleus in the medulla. Cochlear neurons send descending projections to the spinal cord and ascending projections to the pons, thalamus, and cerebellum. Connections to the cerebellum are important for coordinated movements. There are also projections to the temporal cortex, which account for feelings of dizziness; projections to autonomic nervous system areas in the brainstem, which account for motion sickness; and projections to the primary somatosensory cortex, which monitors subjective measurements of the external world and self-movement. People with lesions in the vestibular area of the somatosensory cortex see vertical objects in the world as being tilted. Finally, the vestibular signals project to certain optic muscles to coordinate eye and head movements.

Note:
Link to Learning

Click through this interactive tutorial to review the parts of the ear and how they function to process sound.

Section Summary

Audition is important for territory defense, predation, predator defense, and communal exchanges. The vestibular system, which is not auditory, detects linear acceleration and angular acceleration and deceleration. Both the auditory system and vestibular system use hair cells as their receptors.

Auditory stimuli are sound waves. The sound wave energy reaches the outer ear (pinna, canal, tympanum), and vibrations of the tympanum send the energy to the middle ear. The middle ear bones shift and the stapes transfers mechanical energy to the oval window of the fluid-filled inner ear cochlea. Once in the cochlea, the energy causes the basilar membrane to flex, thereby bending the stereocilia on receptor hair cells. This activates the receptors, which send their auditory neural signals to the brain.

The vestibular system has five parts that work together to provide the sense of direction, thus helping to maintain balance. The utricle and saccule measure head orientation: their calcium carbonate crystals shift when the head is tilted, thereby activating hair cells. The semicircular canals work similarly, such that when the head is turned, the fluid in the canals bends stereocilia on hair cells. The vestibular hair cells also send signals to the thalamus and to somatosensory cortex, but also to the cerebellum, the structure above the brainstem that plays a large role in timing and coordination of movement.

Art Connections

Exercise:

Problem:

[link] Cochlear implants can restore hearing in people who have a nonfunctional cochlear. The implant consists of a microphone that picks up sound. A speech processor selects sounds in the range of human speech, and a transmitter converts these sounds to electrical impulses, which are then sent to the auditory nerve. Which of the following types of hearing loss would not be restored by a cochlear implant?

  a. Hearing loss resulting from absence or loss of hair cells in the organ of Corti.
  b. Hearing loss resulting from an abnormal auditory nerve.
  c. Hearing loss resulting from fracture of the cochlea.
  d. Hearing loss resulting from damage to bones of the middle ear.

Solution:

[link] B

Review Questions

Exercise:

Problem:

In sound, pitch is measured in _____, and volume is measured in _____.

  a. nanometers (nm); decibels (dB)
  b. decibels (dB); nanometers (nm)
  c. decibels (dB); hertz (Hz)
  d. hertz (Hz); decibels (dB)

Solution:

D

Exercise:

Problem: Auditory hair cells are indirectly anchored to the _____.

    a. basilar membrane
    b. oval window
    c. tectorial membrane
    d. ossicles

Solution:

A

Exercise:

Problem:

Which of the following are found both in the auditory system and the vestibular system?

    a. basilar membrane
    b. hair cells
    c. semicircular canals
    d. ossicles

Solution:

B

Free Response

Exercise:

Problem:

How would a rise in altitude likely affect the speed of a sound transmitted through air? Why?

Solution:

The sound would slow down, because it is transmitted through the particles (gas) and there are fewer particles (lower density) at higher altitudes.

Exercise:

Problem:

How might being in a place with less gravity than Earth has (such as Earth's moon) affect vestibular sensation, and why?

Solution:

Because vestibular sensation relies on gravity's effects on tiny crystals in the inner ear, a situation of reduced gravity would likely impair vestibular sensation.

Glossary

audition
    sense of hearing

basilar membrane
    stiff structure in the cochlea that indirectly anchors auditory receptors

cochlea
    whorled structure that contains receptors for transduction of the mechanical wave into an electrical signal

incus
    (also, anvil) second of the three bones of the middle ear

inner ear
    innermost part of the ear; consists of the cochlea and the vestibular
    system

labyrinth
    bony, hollow structure that is the most internal part of the ear; contains
    the sites of transduction of auditory and vestibular information

malleus
    (also, hammer) first of the three bones of the middle ear

middle ear
    part of the hearing apparatus that functions to transfer energy from the
    tympanum to the oval window of the inner ear

organ of Corti
    in the basilar membrane, the site of the transduction of sound, a
    mechanical wave, to a neural signal

ossicle
    one of the three bones of the middle ear

outer ear
    part of the ear that consists of the pinna, ear canal, and tympanum and
    which conducts sound waves into the middle ear

oval window
    thin diaphragm between the middle and inner ears that receives sound
    waves from contact with the stapes bone of the middle ear

pinna
    cartilaginous outer ear

semicircular canal
    one of three half-circular, fluid-filled tubes in the vestibular labyrinth
    that monitors angular acceleration and deceleration

stapes

(also, stirrup) third of the three bones of the middle ear

stereocilia
    in the auditory system, hair-like projections from hair cells that help
    detect sound waves

tectorial membrane
    cochlear structure that lies above the hair cells and participates in the
    transduction of sound at the hair cells

tympanum
    (also, tympanic membrane or ear drum) thin diaphragm between the
    outer and middle ears

ultrasound
    sound frequencies above the human detectable ceiling of
    approximately 20,000 Hz

Vision
By the end of this section, you will be able to:

- Explain how electromagnetic waves differs from sound waves
- Trace the path of light through the eye to the point of the optic nerve
- Explain tonic activity as it is manifested in photoreceptors in the retina

Vision is the ability to detect light patterns from the outside environment and interpret them into images. Animals are bombarded with sensory information, and the sheer volume of visual information can be problematic. Fortunately, the visual systems of species have evolved to attend to the most-important stimuli. The importance of vision to humans is further substantiated by the fact that about one-third of the human cerebral cortex is dedicated to analyzing and perceiving visual information.

Light

As with auditory stimuli, light travels in waves. The compression waves that compose sound must travel in a medium—a gas, a liquid, or a solid. In contrast, light is composed of electromagnetic waves and needs no medium; light can travel in a vacuum ([link]). The behavior of light can be discussed in terms of the behavior of waves and also in terms of the behavior of the fundamental unit of light—a packet of electromagnetic radiation called a photon. A glance at the electromagnetic spectrum shows that visible light for humans is just a small slice of the entire spectrum, which includes radiation that we cannot see as light because it is below the frequency of visible red light and above the frequency of visible violet light.

Certain variables are important when discussing perception of light. Wavelength (which varies inversely with frequency) manifests itself as hue. Light at the red end of the visible spectrum has longer wavelengths (and is lower frequency), while light at the violet end has shorter wavelengths (and is higher frequency). The wavelength of light is expressed in nanometers (nm); one nanometer is one billionth of a meter. Humans perceive light that ranges between approximately 380 nm and 740 nm. Some other animals, though, can detect wavelengths outside of the human range. For example,

bees see near-ultraviolet light in order to locate nectar guides on flowers, and some non-avian reptiles sense infrared light (heat that prey gives off).
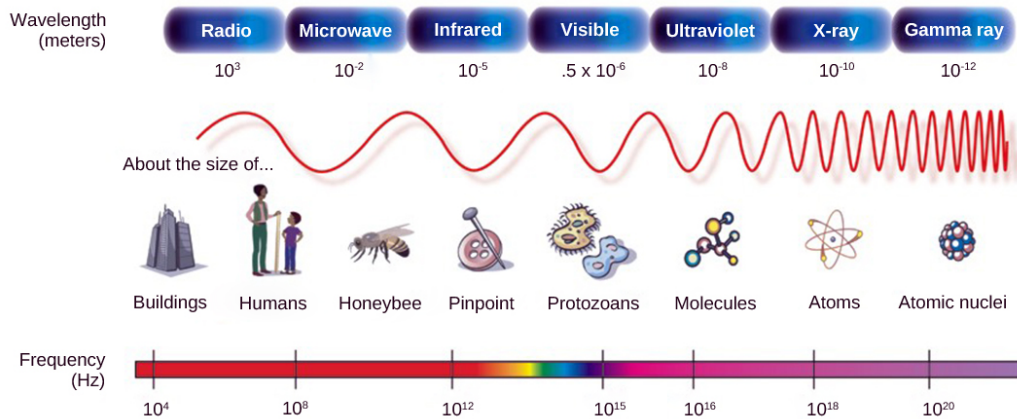
In the electromagnetic spectrum, visible light lies between 380 nm and 740 nm. (credit: modification of work by NASA)

Wave amplitude is perceived as luminous intensity, or brightness. The standard unit of intensity of light is the **candela**, which is approximately the luminous intensity of a one common candle.

Light waves travel 299,792 km per second in a vacuum, (and somewhat slower in various media such as air and water), and those waves arrive at the eye as long (red), medium (green), and short (blue) waves. What is termed "white light" is light that is perceived as white by the human eye. This effect is produced by light that stimulates equally the color receptors in the human eye. The apparent color of an object is the color (or colors) that the object reflects. Thus a red object reflects the red wavelengths in mixed (white) light and absorbs all other wavelengths of light.

Anatomy of the Eye

The photoreceptive cells of the eye, where transduction of light to nervous impulses occurs, are located in the **retina** (shown in [link]) on the inner surface of the back of the eye. But light does not impinge on the retina unaltered. It passes through other layers that process it so that it can be interpreted by the retina ([link]**b**). The **cornea**, the front transparent layer of the eye, and the crystalline **lens**, a transparent convex structure behind the cornea, both refract (bend) light to focus the image on the retina. The **iris**, which is conspicuous as the colored part of the eye, is a circular muscular ring lying between the lens and cornea that regulates the amount of light entering the eye. In conditions of high ambient light, the iris contracts, reducing the size of the pupil at its center. In conditions of low light, the iris relaxes and the pupil enlarges.

Note:
Art Connection

(a) The human eye is shown in cross section. (b) A blowup shows the layers of the retina.

Which of the following statements about the human eye is false?

a. Rods detect color, while cones detect only shades of gray.

The main function of the lens is to focus light on the retina and fovea centralis. The lens is dynamic, focusing and re-focusing light as the eye rests on near and far objects in the visual field. The lens is operated by muscles that stretch it flat or allow it to thicken, changing the focal length of light coming through it to focus it sharply on the retina. With age comes the loss of the flexibility of the lens, and a form of farsightedness called **presbyopia** results. Presbyopia occurs because the image focuses behind the retina. Presbyopia is a deficit similar to a different type of farsightedness called **hyperopia** caused by an eyeball that is too short. For both defects, images in the distance are clear but images nearby are blurry. **Myopia** (nearsightedness) occurs when an eyeball is elongated and the image focus falls in front of the retina. In this case, images in the distance are blurry but images nearby are clear.

There are two types of photoreceptors in the retina: **rods** and **cones**, named for their general appearance as illustrated in [link]. Rods are strongly photosensitive and are located in the outer edges of the retina. They detect dim light and are used primarily for peripheral and nighttime vision. Cones are weakly photosensitive and are located near the center of the retina. They respond to bright light, and their primary role is in daytime, color vision.
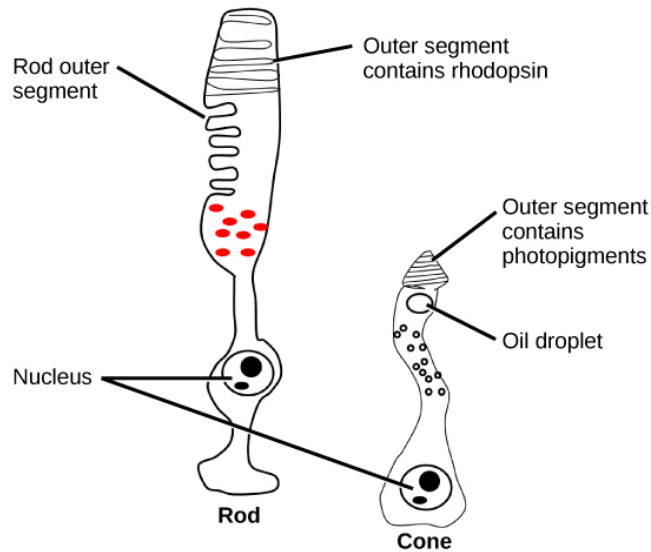
Rods and cones are photoreceptors in the retina. Rods respond in low light and can detect only shades of gray. Cones respond in intense light and are responsible for color vision. (credit: modification of work by Piotr Sliwa)

The **fovea** is the region in the center back of the eye that is responsible for acute vision. The fovea has a high density of cones. When you bring your gaze to an object to examine it intently in bright light, the eyes orient so that the object's image falls on the fovea. However, when looking at a star in the night sky or other object in dim light, the object can be better viewed by the peripheral vision because it is the rods at the edges of the retina, rather than the cones at the center, that operate better in low light. In humans, cones far outnumber rods in the fovea.

Note:
Link to Learning

Review the [anatomical structure](#) of the eye, clicking on each part to practice identification.

Transduction of Light

The rods and cones are the site of transduction of light to a neural signal. Both rods and cones contain photopigments. In vertebrates, the main photopigment, **rhodopsin**, has two main parts [link]): an opsin, which is a membrane protein (in the form of a cluster of α-helices that span the membrane), and retinal—a molecule that absorbs light. When light hits a photoreceptor, it causes a shape change in the retinal, altering its structure from a bent (*cis*) form of the molecule to its linear (*trans*) isomer. This isomerization of retinal activates the rhodopsin, starting a cascade of events that ends with the closing of Na^+ channels in the membrane of the photoreceptor. Thus, unlike most other sensory neurons (which become depolarized by exposure to a stimulus) visual receptors become hyperpolarized and thus driven away from threshold ([link]).

Rhodopsin

Plasma membrane

Retinal

α

Transducin

γ

β

(a)

H₃C CH₃   CH₃

CH₃

H₃C

cis retinal   H   O

H₃C CH₃   CH₃   CH₃ H

CH₃

trans retinal

(b)
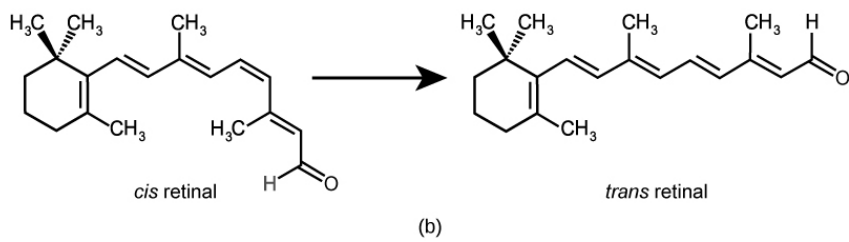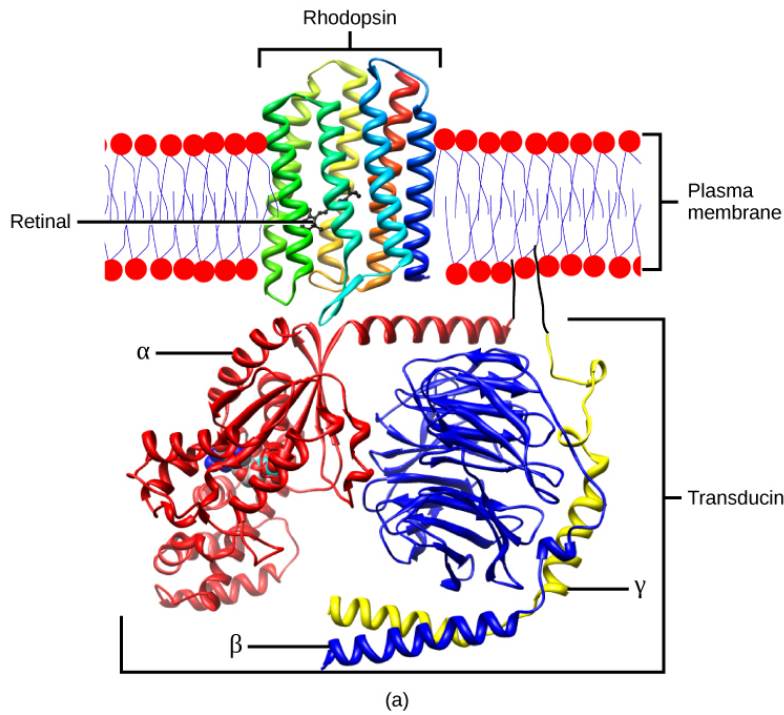
(a) Rhodopsin, the photoreceptor in vertebrates, has two parts: the trans-membrane protein opsin, and retinal. When light strikes retinal, it changes shape from (b) a *cis* to a *trans* form. The signal is passed to a G-protein called transducin, triggering a series of downstream events.
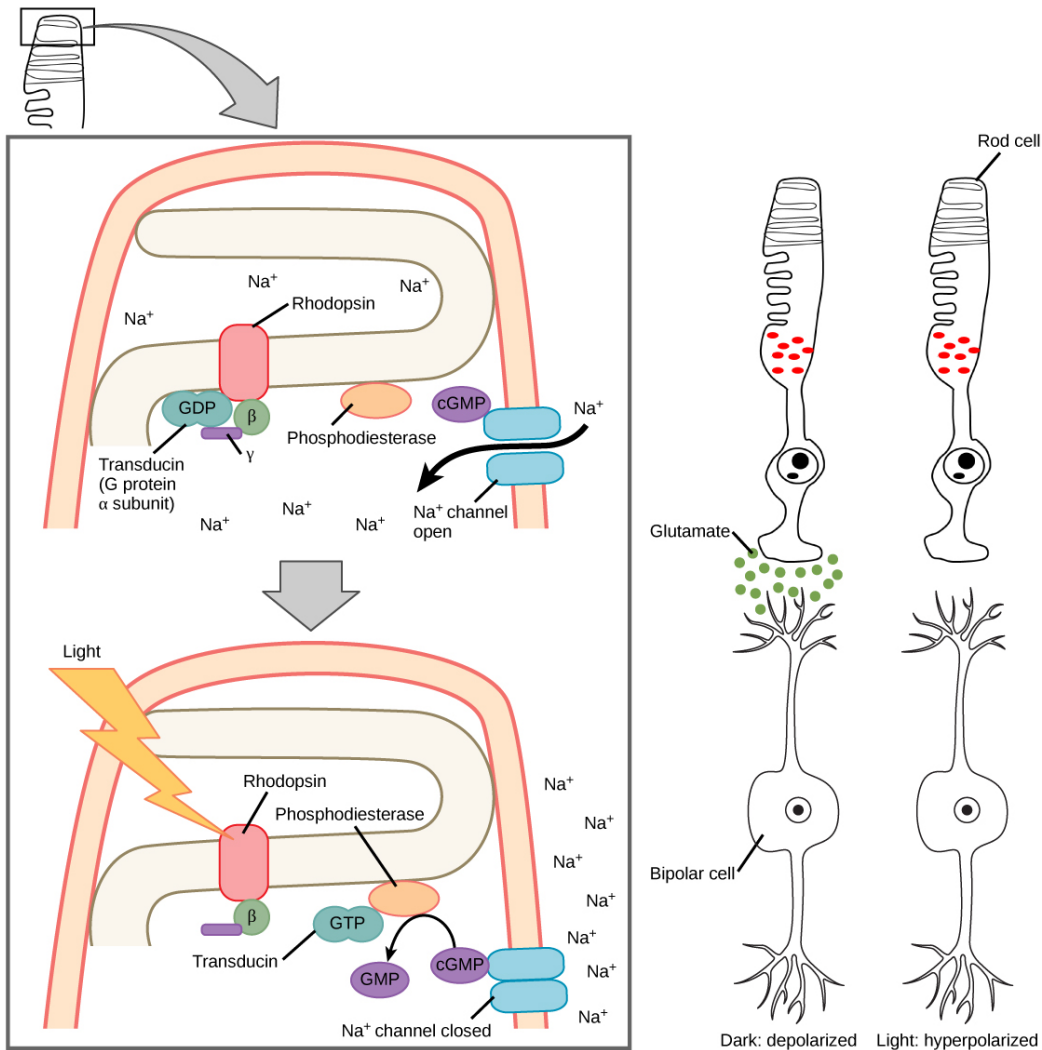
When light strikes rhodopsin, the G-protein transducin is activated, which in turn activates phosphodiesterase. Phosphodiesterase converts cGMP to GMP, thereby closing sodium channels. As a result, the membrane becomes hyperpolarized. The hyperpolarized membrane does not release glutamate to the bipolar cell.

Trichromatic Coding

There are three types of cones (with different photopsins), and they differ in the wavelength to which they are most responsive, as shown in [link]. Some cones are maximally responsive to short light waves of 420 nm, so they are called S cones ("S" for "short"); others respond maximally to waves of 530 nm (M cones, for "medium"); a third group responds maximally to light of longer wavelengths, at 560 nm (L, or "long" cones). With only one type of cone, color vision would not be possible, and a two-cone (dichromatic) system has limitations. Primates use a three-cone (trichromatic) system, resulting in full color vision.

The color we perceive is a result of the ratio of activity of our three types of cones. The colors of the visual spectrum, running from long-wavelength light to short, are red (700 nm), orange (600 nm), yellow (565 nm), green (497 nm), blue (470 nm), indigo (450 nm), and violet (425 nm). Humans have very sensitive perception of color and can distinguish about 500 levels of brightness, 200 different hues, and 20 steps of saturation, or about 2 million distinct colors.
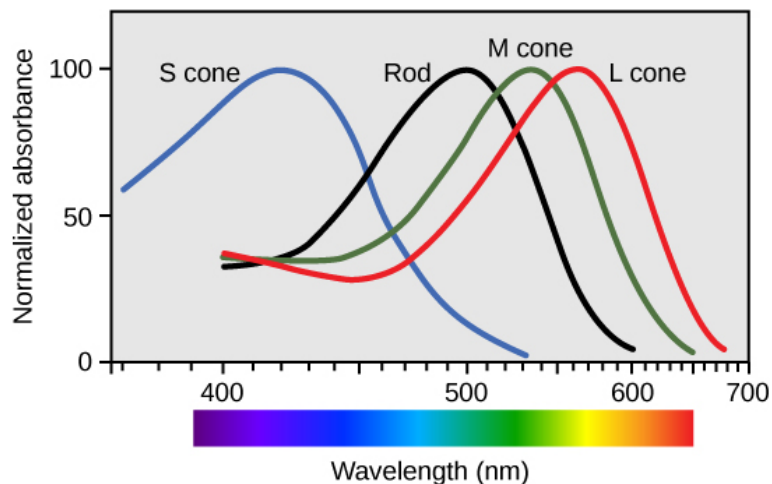
Human rod cells and the different types of cone cells each have an optimal wavelength. However, there is considerable overlap in the wavelengths of light detected.

Retinal Processing

Visual signals leave the cones and rods, travel to the bipolar cells, and then to ganglion cells. A large degree of processing of visual information occurs in the retina itself, before visual information is sent to the brain.

Photoreceptors in the retina continuously undergo **tonic activity**. That is, they are always slightly active even when not stimulated by light. In neurons that exhibit tonic activity, the absence of stimuli maintains a firing rate at a baseline; while some stimuli increase firing rate from the baseline, and other stimuli decrease firing rate. In the absence of light, the bipolar neurons that connect rods and cones to ganglion cells are continuously and actively inhibited by the rods and cones. Exposure of the retina to light hyperpolarizes the rods and cones and removes their inhibition of bipolar cells. The now active bipolar cells in turn stimulate the ganglion cells, which send action potentials along their axons (which leave the eye as the optic nerve). Thus, the visual system relies on change in retinal activity, rather than the absence or presence of activity, to encode visual signals for the brain. Sometimes horizontal cells carry signals from one rod or cone to other photoreceptors and to several bipolar cells. When a rod or cone stimulates a horizontal cell, the horizontal cell inhibits more distant photoreceptors and bipolar cells, creating lateral inhibition. This inhibition sharpens edges and enhances contrast in the images by making regions receiving light appear lighter and dark surroundings appear darker. Amacrine cells can distribute information from one bipolar cell to many ganglion cells.

You can demonstrate this using an easy demonstration to "trick" your retina and brain about the colors you are observing in your visual field. Look fixedly at [link] for about 45 seconds. Then quickly shift your gaze to a sheet of blank white paper or a white wall. You should see an afterimage of the Norwegian flag in its correct colors. At this point, close your eyes for a moment, then reopen them, looking again at the white paper or wall; the afterimage of the flag should continue to appear as red, white, and blue.

What causes this? According to an explanation called opponent process theory, as you gazed fixedly at the green, black, and yellow flag, your retinal ganglion cells that respond positively to green, black, and yellow increased their firing dramatically. When you shifted your gaze to the neutral white ground, these ganglion cells abruptly decreased their activity and the brain interpreted this abrupt downshift as if the ganglion cells were responding now to their "opponent" colors: red, white, and blue, respectively, in the visual field. Once the ganglion cells return to their baseline activity state, the false perception of color will disappear.

View this flag to understand how retinal processing works. Stare at the center of the flag (indicated by the white dot) for 45 seconds, and then quickly look at a white background, noticing how colors appear.

Higher Processing

The myelinated axons of ganglion cells make up the optic nerves. Within the nerves, different axons carry different qualities of the visual signal.

Some axons constitute the magnocellular (big cell) pathway, which carries information about form, movement, depth, and differences in brightness. Other axons constitute the parvocellular (small cell) pathway, which carries information on color and fine detail. Some visual information projects directly back into the brain, while other information crosses to the opposite side of the brain. This crossing of optical pathways produces the distinctive optic chiasma (Greek, for "crossing") found at the base of the brain and allows us to coordinate information from both eyes.

Once in the brain, visual information is processed in several places, and its routes reflect the complexity and importance of visual information to humans and other animals. One route takes the signals to the thalamus, which serves as the routing station for all incoming sensory impulses except olfaction. In the thalamus, the magnocellular and parvocellular distinctions remain intact, and there are different layers of the thalamus dedicated to each. When visual signals leave the thalamus, they travel to the primary visual cortex at the rear of the brain. From the visual cortex, the visual signals travel in two directions. One stream that projects to the parietal lobe, in the side of the brain, carries magnocellular ("where") information. A second stream projects to the temporal lobe and carries both magnocellular ("where") and parvocellular ("what") information.

Another important visual route is a pathway from the retina to the **superior colliculus** in the midbrain, where eye movements are coordinated and integrated with auditory information. Finally, there is the pathway from the retina to the **suprachiasmatic nucleus** (SCN) of the hypothalamus. The SCN is a cluster of cells that is considered to be the body's internal clock, which controls our **circadian** (day-long) cycle. The SCN sends information to the pineal gland, which is important in sleep/wake patterns and annual cycles.

Note:
Link to Learning

View this [interactive presentation](#) to review what you have learned about how vision functions.

Section Summary

Vision is the only photo responsive sense. Visible light travels in waves and is a very small slice of the electromagnetic radiation spectrum. Light waves differ based on their frequency (wavelength = hue) and amplitude (intensity = brightness).

In the vertebrate retina, there are two types of light receptors (photoreceptors): cones and rods. Cones, which are the source of color vision, exist in three forms—L, M, and S—and they are differentially sensitive to different wavelengths. Cones are located in the retina, along with the dim-light, achromatic receptors (rods). Cones are found in the fovea, the central region of the retina, whereas rods are found in the peripheral regions of the retina.

Visual signals travel from the eye over the axons of retinal ganglion cells, which make up the optic nerves. Ganglion cells come in several versions. Some ganglion cell axons carry information on form, movement, depth, and brightness, while other axons carry information on color and fine detail. Visual information is sent to the superior colliculi in the midbrain, where coordination of eye movements and integration of auditory information takes place. Visual information is also sent to the suprachiasmatic nucleus (SCN) of the hypothalamus, which plays a role in the circadian cycle.

Art Connections

Exercise:

  Problem:

  Which of the following statements about the human eye is false?

    a. Rods detect color, while cones detect only shades of gray.
    b. When light enters the retina, it passes the ganglion cells and
       bipolar cells before reaching photoreceptors at the rear of the eye.
    c. The iris adjusts the amount of light coming into the eye.
    d. The cornea is a protective layer on the front of the eye.

  Solution:

  A

Review Questions

Exercise:

  Problem: Why do people over 55 often need reading glasses?

    a. Their cornea no longer focuses correctly.
    b. Their lens no longer focuses correctly.
    c. Their eyeball has elongated with age, causing images to focus in
       front of their retina.
    d. Their retina has thinned with age, making vision more difficult.

  Solution:

  B

Exercise:

Problem:

Why is it easier to see images at night using peripheral, rather than the central, vision?

   a. Cones are denser in the periphery of the retina.
   b. Bipolar cells are denser in the periphery of the retina.
   c. Rods are denser in the periphery of the retina.
   d. The optic nerve exits at the periphery of the retina.

Solution:

C

Exercise:

Problem:

A person catching a ball must coordinate her head and eyes. What part of the brain is helping to do this?

   a. hypothalamus
   b. pineal gland
   c. thalamus
   d. superior colliculus

Solution:

D

Free Response

Exercise:

Problem:

How could the pineal gland, the brain structure that plays a role in annual cycles, use visual information from the suprachiasmatic nucleus of the hypothalamus?

Solution:

The pineal gland could use length-of-day information to determine the time of year, for example. Day length is shorter in the winter than it is in the summer. For many animals and plants, photoperiod cues them to reproduce at a certain time of year.

Exercise:

Problem:

How is the relationship between photoreceptors and bipolar cells different from other sensory receptors and adjacent cells?

Solution:

The photoreceptors tonically inhibit the bipolar cells, and stimulation of the receptors turns this inhibition off, activating the bipolar cells.

Glossary

candela
    (cd) unit of measurement of luminous intensity (brightness)

circadian
    describes a time cycle about one day in length

cone
    weakly photosensitive, chromatic, cone-shaped neuron in the fovea of the retina that detects bright light and is used in daytime color vision

cornea

transparent layer over the front of the eye that helps focus light waves

fovea
    region in the center of the retina with a high density of photoreceptors
    and which is responsible for acute vision

hyperopia
    (also, farsightedness) visual defect in which the image focus falls
    behind the retina, thereby making images in the distance clear, but
    close-up images blurry

iris
    pigmented, circular muscle at the front of the eye that regulates the
    amount of light entering the eye

lens
    transparent, convex structure behind the cornea that helps focus light
    waves on the retina

myopia
    (also, nearsightedness) visual defect in which the image focus falls in
    front of the retina, thereby making images in the distance blurry, but
    close-up images clear

presbyopia
    visual defect in which the image focus falls behind the retina, thereby
    making images in the distance clear, but close-up images blurry;
    caused by age-based changes in the lens

pupil
    small opening though which light enters

retina
    layer of photoreceptive and supporting cells on the inner surface of the
    back of the eye

rhodopsin
    main photopigment in vertebrates

rod
> strongly photosensitive, achromatic, cylindrical neuron in the outer edges of the retina that detects dim light and is used in peripheral and nighttime vision

superior colliculus
> paired structure in the top of the midbrain, which manages eye movements and auditory integration

suprachiasmatic nucleus
> cluster of cells in the hypothalamus that plays a role in the circadian cycle

tonic activity
> in a neuron, slight continuous activity while at rest

vision
> sense of sight

Introduction class="introduction"

Just as humans recycle what we can and dump the remains into landfills, our bodies use and recycle what they can and excrete the remaining waste products. Our bodies' complex systems have developed ways to treat waste and maintain a balanced internal environment. (credit: modification of work by Redwin Law)

The daily intake recommendation for human water consumption is eight to ten glasses of water. In order to achieve a healthy balance, the human body should excrete the eight to ten glasses of water every day. This occurs via the processes of urination, defecation, sweating and, to a small extent, respiration. The organs and tissues of the human body are soaked in fluids that are maintained at constant temperature, pH, and solute concentration, all crucial elements of homeostasis. The solutes in body fluids are mainly mineral salts and sugars, and osmotic regulation is the process by which the mineral salts and water are kept in balance. Osmotic homeostasis is maintained despite the influence of external factors like temperature, diet, and weather conditions.

Osmoregulation and Osmotic Balance
By the end of this section, you will be able to:

- Define osmosis and explain its role within molecules
- Explain why osmoregulation and osmotic balance are important body functions
- Describe active transport mechanisms
- Explain osmolarity and the way in which it is measured
- Describe osmoregulators or osmoconformers and how these tools allow animals to adapt to different environments

Osmosis is the diffusion of water across a membrane in response to **osmotic pressure** caused by an imbalance of molecules on either side of the membrane. **Osmoregulation** is the process of maintenance of salt and water balance (**osmotic balance**) across membranes within the body's fluids, which are composed of water, plus electrolytes and non-electrolytes. An **electrolyte** is a solute that dissociates into ions when dissolved in water. A **non-electrolyte**, in contrast, doesn't dissociate into ions during water dissolution. Both electrolytes and non-electrolytes contribute to the osmotic balance. The body's fluids include blood plasma, the cytosol within cells, and interstitial fluid, the fluid that exists in the spaces between cells and tissues of the body. The membranes of the body (such as the pleural, serous, and cell membranes) are **semi-permeable membranes**. Semi-permeable membranes are permeable (or permissive) to certain types of solutes and water. Solutions on two sides of a semi-permeable membrane tend to equalize in solute concentration by movement of solutes and/or water across the membrane. As seen in [link], a cell placed in water tends to swell due to gain of water from the hypotonic or "low salt" environment. A cell placed in a solution with higher salt concentration, on the other hand, tends to make the membrane shrivel up due to loss of water into the hypertonic or "high salt" environment. Isotonic cells have an equal concentration of solutes inside and outside the cell; this equalizes the osmotic pressure on either side of the cell membrane which is a semi-permeable membrane.

Hypertonic solution   Isotonic solution   Hypotonic solution
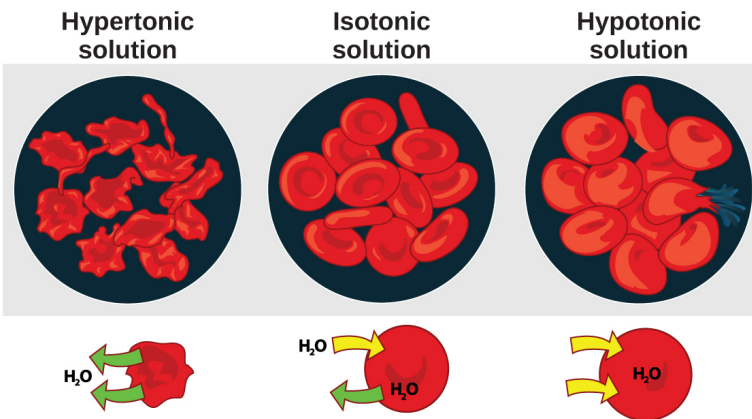
Cells placed in a hypertonic environment tend to shrink due to loss of water. In a hypotonic environment, cells tend to swell due to intake of water. The blood maintains an isotonic environment so that cells neither shrink nor swell. (credit: Mariana Ruiz Villareal)

The body does not exist in isolation. There is a constant input of water and electrolytes into the system. While osmoregulation is achieved across membranes within the body, excess electrolytes and wastes are transported to the kidneys and excreted, helping to maintain osmotic balance.

Need for Osmoregulation

Biological systems constantly interact and exchange water and nutrients with the environment by way of consumption of food and water and through excretion in the form of sweat, urine, and feces. Without a mechanism to regulate osmotic pressure, or when a disease damages this mechanism, there is a tendency to accumulate toxic waste and water, which can have dire consequences.

Mammalian systems have evolved to regulate not only the overall osmotic pressure across membranes, but also specific concentrations of important electrolytes in the three major fluid compartments: blood plasma,

extracellular fluid, and intracellular fluid. Since osmotic pressure is regulated by the movement of water across membranes, the volume of the fluid compartments can also change temporarily. Because blood plasma is one of the fluid components, osmotic pressures have a direct bearing on blood pressure.

Transport of Electrolytes across Cell Membranes

Electrolytes, such as sodium chloride, ionize in water, meaning that they dissociate into their component ions. In water, sodium chloride (NaCl), dissociates into the sodium ion (Na^+) and the chloride ion (Cl^-). The most important ions, whose concentrations are very closely regulated in body fluids, are the cations sodium (Na^+), potassium (K^+), calcium (Ca^{+2}), magnesium (Mg^{+2}), and the anions chloride (Cl^-), carbonate (CO_3^{-2}), bicarbonate (HCO_3^-), and phosphate(PO_3^-). Electrolytes are lost from the body during urination and perspiration. For this reason, athletes are encouraged to replace electrolytes and fluids during periods of increased activity and perspiration.

Osmotic pressure is influenced by the concentration of solutes in a solution. It is directly proportional to the number of solute atoms or molecules and not dependent on the size of the solute molecules. Because electrolytes dissociate into their component ions, they, in essence, add more solute particles into the solution and have a greater effect on osmotic pressure, per mass than compounds that do not dissociate in water, such as glucose.

Water can pass through membranes by passive diffusion. If electrolyte ions could passively diffuse across membranes, it would be impossible to maintain specific concentrations of ions in each fluid compartment therefore they require special mechanisms to cross the semi-permeable membranes in the body. This movement can be accomplished by facilitated diffusion and active transport. Facilitated diffusion requires protein-based channels for moving the solute. Active transport requires energy in the form of ATP conversion, carrier proteins, or pumps in order to move ions against the concentration gradient.

Concept of Osmolality and Milliequivalent

In order to calculate osmotic pressure, it is necessary to understand how solute concentrations are measured. The unit for measuring solutes is the **mole**. One mole is defined as the gram molecular weight of the solute. For example, the molecular weight of sodium chloride is 58.44. Thus, one mole of sodium chloride weighs 58.44 grams. The **molarity** of a solution is the number of moles of solute per liter of solution. The **molality** of a solution is the number of moles of solute per kilogram of solvent. If the solvent is water, one kilogram of water is equal to one liter of water. While molarity and molality are used to express the concentration of solutions, electrolyte concentrations are usually expressed in terms of milliequivalents per liter (mEq/L): the mEq/L is equal to the ion concentration (in millimoles) multiplied by the number of electrical charges on the ion. The unit of milliequivalent takes into consideration the ions present in the solution (since electrolytes form ions in aqueous solutions) and the charge on the ions.

Thus, for ions that have a charge of one, one milliequivalent is equal to one millimole. For ions that have a charge of two (like calcium), one milliequivalent is equal to 0.5 millimoles. Another unit for the expression of electrolyte concentration is the milliosmole (mOsm), which is the number of milliequivalents of solute per kilogram of solvent. Body fluids are usually maintained within the range of 280 to 300 mOsm.

Osmoregulators and Osmoconformers

Persons lost at sea without any fresh water to drink are at risk of severe dehydration because the human body cannot adapt to drinking seawater, which is hypertonic in comparison to body fluids. Organisms such as goldfish that can tolerate only a relatively narrow range of salinity are referred to as stenohaline. About 90 percent of all bony fish are restricted to either freshwater or seawater. They are incapable of osmotic regulation in the opposite environment. It is possible, however, for a few fishes like salmon to spend part of their life in fresh water and part in sea water. Organisms like the salmon and molly that can tolerate a relatively wide range of salinity are referred to as euryhaline organisms. This is possible because some fish have evolved **osmoregulatory** mechanisms to survive in all kinds of aquatic environments. When they live in fresh water, their

bodies tend to take up water because the environment is relatively hypotonic, as illustrated in [link]**a**. In such hypotonic environments, these fish do not drink much water. Instead, they pass a lot of very dilute urine, and they achieve electrolyte balance by active transport of salts through the gills. When they move to a hypertonic marine environment, these fish start drinking sea water; they excrete the excess salts through their gills and their urine, as illustrated in [link]**b**. Most marine invertebrates, on the other hand, may be isotonic with sea water (**osmoconformers**). Their body fluid concentrations conform to changes in seawater concentration. Cartilaginous fishes' salt composition of the blood is similar to bony fishes; however, the blood of sharks contains the organic compounds urea and trimethylamine oxide (TMAO). This does not mean that their electrolyte composition is similar to that of sea water. They achieve isotonicity with the sea by storing large concentrations of urea. These animals that secrete urea are called ureotelic animals. TMAO stabilizes proteins in the presence of high urea levels, preventing the disruption of peptide bonds that would occur in other animals exposed to similar levels of urea. Sharks are cartilaginous fish with a rectal gland to secrete salt and assist in osmoregulation.
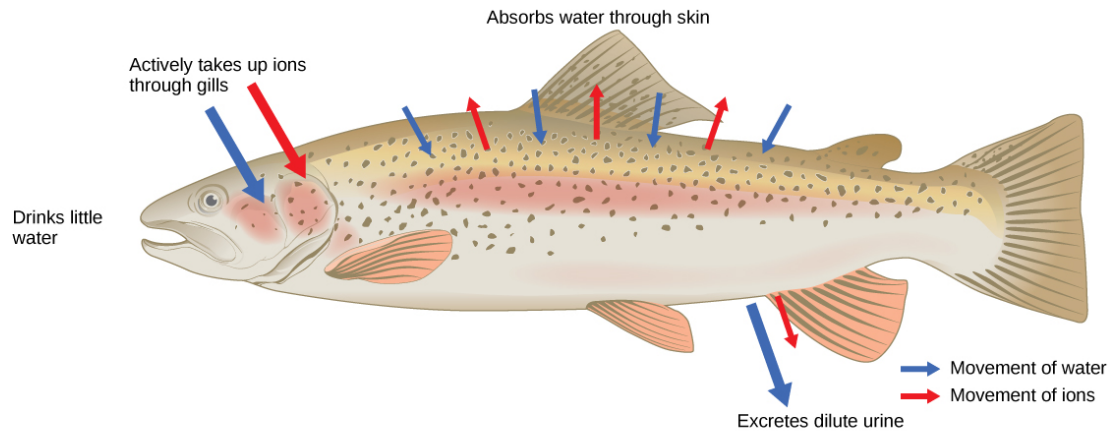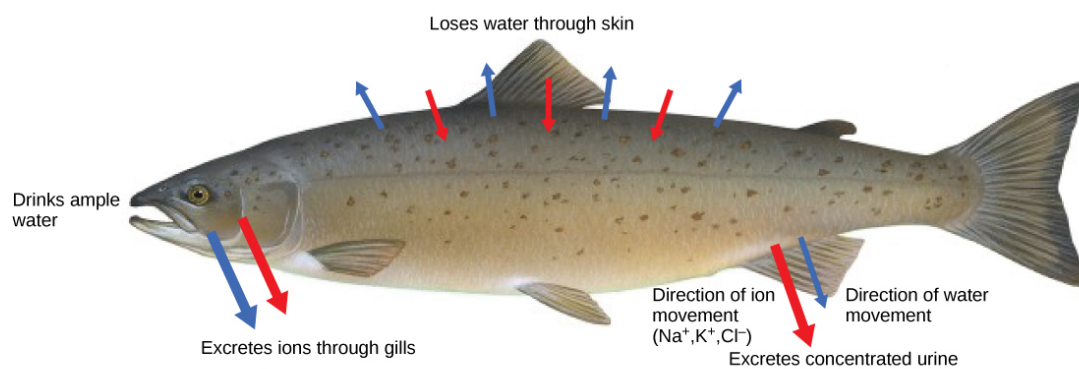
Fish are osmoregulators, but must use different mechanisms to survive in (a) freshwater or (b) saltwater environments. (credit: modification of work by Duane Raver, NOAA)

Note:
Career Connection
Dialysis Technician
Dialysis is a medical process of removing wastes and excess water from the blood by diffusion and ultrafiltration. When kidney function fails, dialysis must be done to artificially rid the body of wastes. This is a vital process to keep patients alive. In some cases, the patients undergo artificial dialysis until they are eligible for a kidney transplant. In others who are not candidates for kidney transplants, dialysis is a life-long necessity.

Dialysis technicians typically work in hospitals and clinics. While some roles in this field include equipment development and maintenance, most dialysis technicians work in direct patient care. Their on-the-job duties, which typically occur under the direct supervision of a registered nurse, focus on providing dialysis treatments. This can include reviewing patient history and current condition, assessing and responding to patient needs before and during treatment, and monitoring the dialysis process. Treatment may include taking and reporting a patient's vital signs and preparing solutions and equipment to ensure accurate and sterile procedures.

Section Summary

Solute concentrations across a semi-permeable membranes influence the movement of water and solutes across the membrane. It is the number of solute molecules and not the molecular size that is important in osmosis. Osmoregulation and osmotic balance are important bodily functions, resulting in water and salt balance. Not all solutes can pass through a semi-permeable membrane. Osmosis is the movement of water across the membrane. Osmosis occurs to equalize the number of solute molecules across a semi-permeable membrane by the movement of water to the side of higher solute concentration. Facilitated diffusion utilizes protein channels to move solute molecules from areas of higher to lower concentration while active transport mechanisms are required to move solutes against concentration gradients. Osmolarity is measured in units of milliequivalents or milliosmoles, both of which take into consideration the number of solute particles and the charge on them. Fish that live in fresh water or saltwater adapt by being osmoregulators or osmoconformers.

Review Questions

Exercise:

Problem:

When a dehydrated human patient needs to be given fluids intravenously, he or she is given:

   a. water, which is hypotonic with respect to body fluids
   b. saline at a concentration that is isotonic with respect to body fluids
   c. glucose because it is a non-electrolyte
   d. blood

Solution:

B

Exercise:

Problem: The sodium ion is at the highest concentration in:

   a. intracellular fluid
   b. extracellular fluid
   c. blood plasma
   d. none of the above

Solution:

B

Exercise:

Problem: Cells in a hypertonic solution tend to:

   a. shrink due to water loss
   b. swell due to water gain
   c. stay the same size due to water moving into and out of the cell at the same rate

    d. none of the above

Solution:

A

Free Response

Exercise:

Problem:

Why is excretion important in order to achieve osmotic balance?

Solution:

Excretion allows an organism to rid itself of waste molecules that could be toxic if allowed to accumulate. It also allows the organism to keep the amount of water and dissolved solutes in balance.

Exercise:

Problem:

Why do electrolyte ions move across membranes by active transport?

Solution:

Electrolyte ions often require special mechanisms to cross the semi-permeable membranes in the body. Active transport is the movement against a concentration gradient.

Glossary

electrolyte
    solute that breaks down into ions when dissolved in water

molality
    number of moles of solute per kilogram of solvent

molarity
    number of moles of solute per liter of solution

mole
    gram equivalent of the molecular weight of a substance

non-electrolyte
    solute that does not break down into ions when dissolved in water

osmoconformer
    organism that changes its tonicity based on its environment

osmoregulation
    mechanism by which water and solute concentrations are maintained at
    desired levels

osmoregulator
    organism that maintains its tonicity irrespective of its environment

osmotic balance
    balance of the amount of water and salt input and output to and from a
    biological system without disturbing the desired osmotic pressure and
    solute concentration in every compartment

osmotic pressure
    pressure exerted on a membrane to equalize solute concentration on
    either side

semi-permeable membrane
    membrane that allows only certain solutes to pass through

The Kidneys and Osmoregulatory Organs
By the end of this section, you will be able to:

- Explain how the kidneys serve as the main osmoregulatory organs in mammalian systems
- Describe the structure of the kidneys and the functions of the parts of the kidney
- Describe how the nephron is the functional unit of the kidney and explain how it actively filters blood and generates urine
- Detail the three steps in the formation of urine: glomerular filtration, tubular reabsorption, and tubular secretion

Although the kidneys are the major osmoregulatory organ, the skin and lungs also play a role in the process. Water and electrolytes are lost through sweat glands in the skin, which helps moisturize and cool the skin surface, while the lungs expel a small amount of water in the form of mucous secretions and via evaporation of water vapor.

Kidneys: The Main Osmoregulatory Organ

The **kidneys**, illustrated in [link], are a pair of bean-shaped structures that are located just below and posterior to the liver in the peritoneal cavity. The adrenal glands sit on top of each kidney and are also called the suprarenal glands. Kidneys filter blood and purify it. All the blood in the human body is filtered many times a day by the kidneys; these organs use up almost 25 percent of the oxygen absorbed through the lungs to perform this function. Oxygen allows the kidney cells to efficiently manufacture chemical energy in the form of ATP through aerobic respiration. The filtrate coming out of the kidneys is called **urine**.
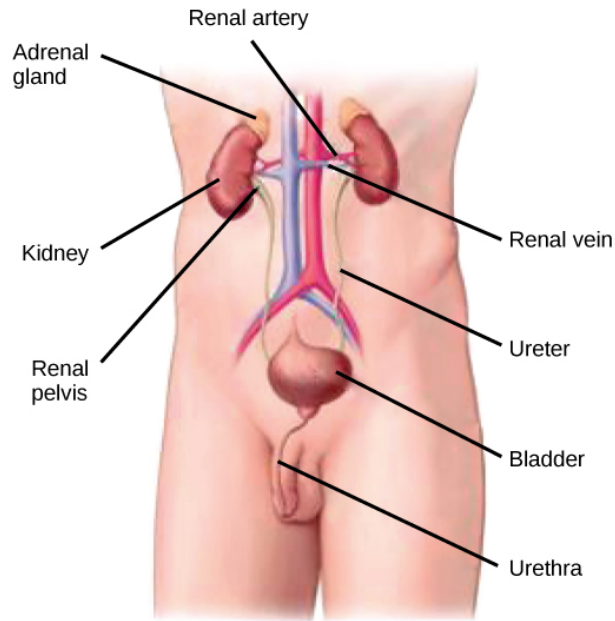
Kidneys filter the blood, producing urine that is stored in the bladder prior to elimination through the urethra. (credit: modification of work by NCI)

Kidney Structure

Externally, the kidneys are surrounded by three layers, illustrated in [link]. The outermost layer is a tough connective tissue layer called the **renal fascia**. The second layer is called the **perirenal fat capsule**, which helps anchor the kidneys in place. The third and innermost layer is the **renal capsule**. Internally, the kidney has three regions—an outer **cortex**, a **medulla** in the middle, and the **renal pelvis** in the region called the **hilum** of the kidney. The hilum is the concave part of the bean-shape where blood vessels and nerves enter and exit the kidney; it is also the point of exit for the ureters. The renal cortex is granular due to the presence of **nephrons**—the functional unit of the kidney. The medulla consists of multiple pyramidal tissue masses, called the **renal pyramids**. In between the pyramids are spaces called **renal columns** through which the blood vessels

pass. The tips of the pyramids, called renal papillae, point toward the renal pelvis. There are, on average, eight renal pyramids in each kidney. The renal pyramids along with the adjoining cortical region are called the **lobes of the kidney**. The renal pelvis leads to the **ureter** on the outside of the kidney. On the inside of the kidney, the renal pelvis branches out into two or three extensions called the major **calyces**, which further branch into the minor calyces. The ureters are urine-bearing tubes that exit the kidney and empty into the **urinary bladder**.

Note:
Art Connection
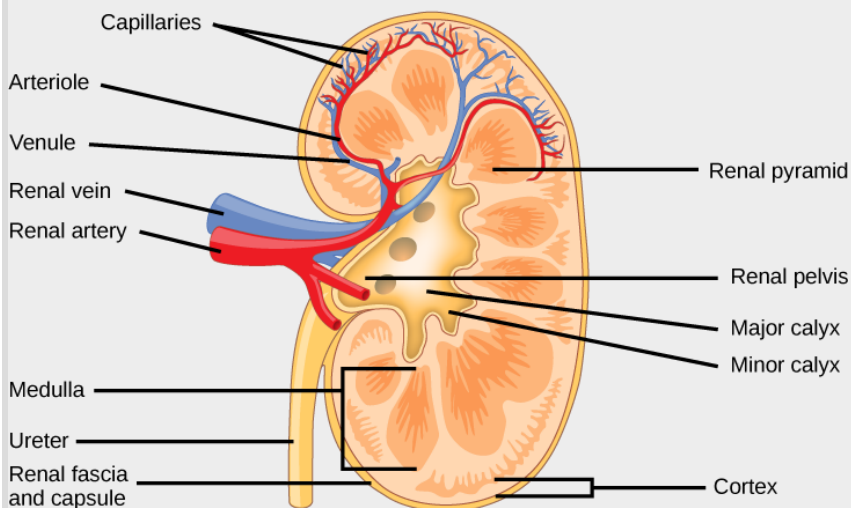
The internal structure of the kidney is shown. (credit: modification of work by NCI)

Which of the following statements about the kidney is false?

a. The renal pelvis drains into the ureter.
b. The renal pyramids are in the medulla.
c. The cortex covers the capsule.
d. Nephrons are in the renal cortex.

Because the kidney filters blood, its network of blood vessels is an important component of its structure and function. The arteries, veins, and nerves that supply the kidney enter and exit at the renal hilum. Renal blood supply starts with the branching of the aorta into the **renal arteries** (which are each named based on the region of the kidney they pass through) and ends with the exiting of the **renal veins** to join the **inferior vena cava**. The renal arteries split into several **segmental arteries** upon entering the kidneys. Each segmental artery splits further into several **interlobar arteries** and enters the renal columns, which supply the renal lobes. The interlobar arteries split at the junction of the renal cortex and medulla to form the **arcuate arteries**. The arcuate "bow shaped" arteries form arcs along the base of the medullary pyramids. **Cortical radiate arteries**, as the name suggests, radiate out from the arcuate arteries. The cortical radiate arteries branch into numerous afferent arterioles, and then enter the capillaries supplying the nephrons. Veins trace the path of the arteries and have similar names, except there are no segmental veins.

As mentioned previously, the functional unit of the kidney is the nephron, illustrated in [link]. Each kidney is made up of over one million nephrons that dot the renal cortex, giving it a granular appearance when sectioned sagittally. There are two types of nephrons—**cortical nephrons** (85 percent), which are deep in the renal cortex, and **juxtamedullary nephrons** (15 percent), which lie in the renal cortex close to the renal medulla. A nephron consists of three parts—a **renal corpuscle**, a **renal tubule**, and the associated capillary network, which originates from the cortical radiate arteries.

Note:
Art Connection
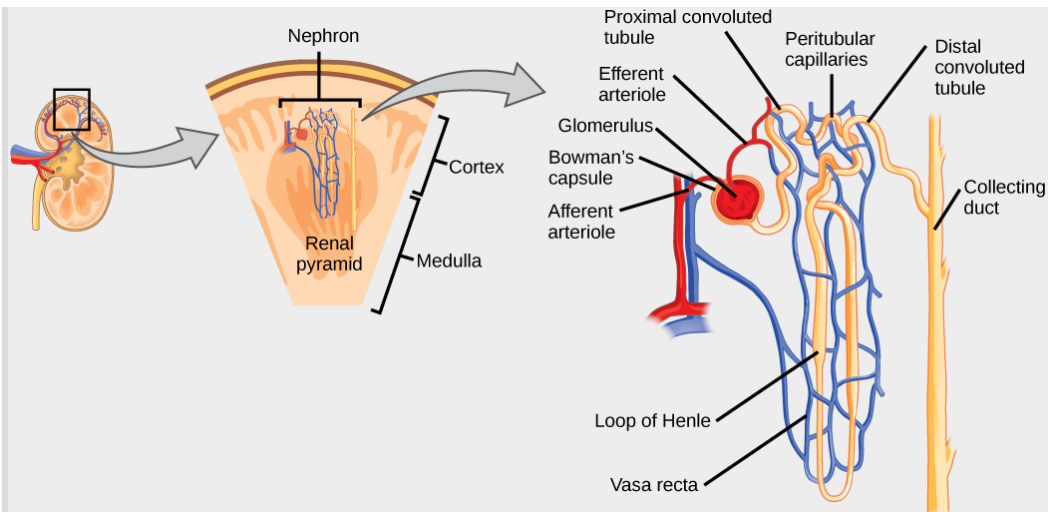
The nephron is the functional unit of the kidney. The glomerulus and convoluted tubules are located in the kidney cortex, while collecting ducts are located in the pyramids of the medulla. (credit: modification of work by NIDDK)

Which of the following statements about the nephron is false?

a. The collecting duct empties into the distal convoluted tubule.
b. The Bowman's capsule surrounds the glomerulus.
c. The loop of Henle is between the proximal and distal convoluted tubules.
d. The loop of Henle empties into the distal convoluted tubule.

Renal Corpuscle

The renal corpuscle, located in the renal cortex, is made up of a network of capillaries known as the **glomerulus** and the capsule, a cup-shaped chamber that surrounds it, called the glomerular or **Bowman's capsule**.

Renal Tubule

The renal tubule is a long and convoluted structure that emerges from the glomerulus and can be divided into three parts based on function. The first part is called the **proximal convoluted tubule (PCT)** due to its proximity to the glomerulus; it stays in the renal cortex. The second part is called the **loop of Henle**, or nephritic loop, because it forms a loop (with **descending** and **ascending limbs**) that goes through the renal medulla. The third part of the renal tubule is called the **distal convoluted tubule (DCT)** and this part is also restricted to the renal cortex. The DCT, which is the last part of the nephron, connects and empties its contents into collecting ducts that line the medullary pyramids. The collecting ducts amass contents from multiple nephrons and fuse together as they enter the papillae of the renal medulla.

Capillary Network within the Nephron

The capillary network that originates from the renal arteries supplies the nephron with blood that needs to be filtered. The branch that enters the glomerulus is called the **afferent arteriole**. The branch that exits the glomerulus is called the **efferent arteriole**. Within the glomerulus, the network of capillaries is called the glomerular capillary bed. Once the efferent arteriole exits the glomerulus, it forms the **peritubular capillary network**, which surrounds and interacts with parts of the renal tubule. In cortical nephrons, the peritubular capillary network surrounds the PCT and DCT. In juxtamedullary nephrons, the peritubular capillary network forms a network around the loop of Henle and is called the **vasa recta**.

Note:
Link to Learning

Go to [this website](#) to see another coronal section of the kidney and to explore an animation of the workings of nephrons.

Kidney Function and Physiology

Kidneys filter blood in a three-step process. First, the nephrons filter blood that runs through the capillary network in the glomerulus. Almost all solutes, except for proteins, are filtered out into the glomerulus by a process called **glomerular filtration**. Second, the filtrate is collected in the renal tubules. Most of the solutes get reabsorbed in the PCT by a process called **tubular reabsorption**. In the loop of Henle, the filtrate continues to exchange solutes and water with the renal medulla and the peritubular capillary network. Water is also reabsorbed during this step. Then, additional solutes and wastes are secreted into the kidney tubules during **tubular secretion**, which is, in essence, the opposite process to tubular reabsorption. The collecting ducts collect filtrate coming from the nephrons and fuse in the medullary papillae. From here, the papillae deliver the filtrate, now called urine, into the minor calyces that eventually connect to the ureters through the renal pelvis. This entire process is illustrated in [link].

2. Proximal convoluted tubule: reabsorbs ions, water, and nutrients; removes toxins and adjusts filtrate pH

5. Distal tubule: selectively secretes and absorbs different ions to maintain blood pH and electrolyte balance

1. Glomerulus: filters small solutes from the blood

6. Collecting duct: reabsorbs solutes and water from the filtrate

4. Ascending loop of Henle: reabsorbs Na^+ and Cl^- from the filtrate into the interstitial fluid

3. Descending loop of Henle: aquaporins allow water to pass from the filtrate into the interstitial fluid

Each part of the nephron performs a different function in filtering waste and maintaining homeostatic balance. (1) The glomerulus forces small solutes out of the blood by pressure. (2) The proximal convoluted tubule reabsorbs ions, water, and nutrients from the filtrate into the interstitial fluid, and actively transports toxins and drugs from the interstitial fluid into the filtrate. The proximal convoluted tubule also adjusts blood pH by selectively secreting ammonia (NH_3) into the filtrate, where it reacts with H^+ to form NH_4^+. The more acidic the filtrate, the more ammonia is secreted. (3) The descending loop of Henle is lined

with cells containing aquaporins that allow water to pass from the filtrate into the interstitial fluid. (4) In the thin part of the ascending loop of Henle, Na^+ and Cl^- ions diffuse into the interstitial fluid. In the thick part, these same ions are actively transported into the interstitial fluid. Because salt but not water is lost, the filtrate becomes more dilute as it travels up the limb. (5) In the distal convoluted tubule, K^+ and H^+ ions are selectively secreted into the filtrate, while Na^+, Cl^-, and HCO_3^- ions are reabsorbed to maintain pH and electrolyte balance in the blood. (6) The collecting duct reabsorbs solutes and water from the filtrate, forming dilute urine. (credit: modification of work by NIDDK)

Glomerular Filtration

Glomerular filtration filters out most of the solutes due to high blood pressure and specialized membranes in the afferent arteriole. The blood pressure in the glomerulus is maintained independent of factors that affect systemic blood pressure. The "leaky" connections between the endothelial cells of the glomerular capillary network allow solutes to pass through easily. All solutes in the glomerular capillaries, except for macromolecules like proteins, pass through by passive diffusion. There is no energy requirement at this stage of the filtration process. **Glomerular filtration**

rate (GFR) is the volume of glomerular filtrate formed per minute by the kidneys. GFR is regulated by multiple mechanisms and is an important indicator of kidney function.

Tubular Reabsorption and Secretion

Tubular reabsorption occurs in the PCT part of the renal tubule. Almost all nutrients are reabsorbed, and this occurs either by passive or active transport. Reabsorption of water and some key electrolytes are regulated and can be influenced by hormones. Sodium (Na^+) is the most abundant ion and most of it is reabsorbed by active transport and then transported to the peritubular capillaries. Because Na^+ is actively transported out of the tubule, water follows it to even out the osmotic pressure. Water is also independently reabsorbed into the peritubular capillaries due to the presence of aquaporins, or water channels, in the PCT. This occurs due to the low blood pressure and high osmotic pressure in the peritubular capillaries. However, every solute has a **transport maximum** and the excess is not reabsorbed.

In the loop of Henle, the permeability of the membrane changes. The descending limb is permeable to water, not solutes; the opposite is true for the ascending limb. Additionally, the loop of Henle invades the renal

medulla, which is naturally high in salt concentration and tends to absorb water from the renal tubule and concentrate the filtrate. The osmotic gradient increases as it moves deeper into the medulla. Because two sides of the loop of Henle perform opposing functions, as illustrated in [link], it acts as a **countercurrent multiplier**. The vasa recta around it acts as the **countercurrent exchanger**.

Note:
Art Connection
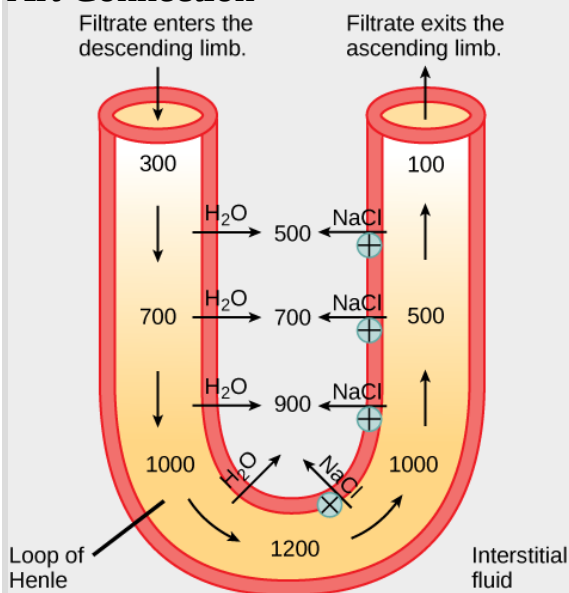
The loop of Henle acts as a countercurrent multiplier that uses energy to create concentration gradients. The descending limb is water permeable. Water flows from the filtrate to the interstitial fluid, so osmolality inside the limb increases as it descends into the renal medulla. At the bottom, the osmolality is higher inside the loop than in

the interstitial fluid. Thus, as filtrate enters the ascending limb, Na^+ and Cl^- ions exit through ion channels present in the cell membrane. Further up, Na^+ is actively transported out of the filtrate and Cl^- follows. Osmolarity is given in units of milliosmoles per liter (mOsm/L).

Loop diuretics are drugs sometimes used to treat hypertension. These drugs inhibit the reabsorption of Na^+ and Cl^- ions by the ascending limb of the loop of Henle. A side effect is that they increase urination. Why do you think this is the case?

By the time the filtrate reaches the DCT, most of the urine and solutes have been reabsorbed. If the body requires additional water, all of it can be reabsorbed at this point. Further reabsorption is controlled by hormones, which will be discussed in a later section. Excretion of wastes occurs due to lack of reabsorption combined with tubular secretion. Undesirable products like metabolic wastes, urea, uric acid, and certain drugs, are excreted by tubular secretion. Most of the tubular secretion happens in the DCT, but some occurs in the early part of the collecting duct. Kidneys also maintain an acid-base balance by secreting excess H^+ ions.

Although parts of the renal tubules are named proximal and distal, in a cross-section of the kidney, the tubules are placed close together and in contact with each other and the glomerulus. This allows for exchange of chemical messengers between the different cell types. For example, the DCT ascending limb of the loop of Henle has masses of cells called **macula densa**, which are in contact with cells of the afferent arterioles called **juxtaglomerular cells**. Together, the macula densa and juxtaglomerular

cells form the juxtaglomerular complex (JGC). The JGC is an endocrine structure that secretes the enzyme renin and the hormone erythropoietin. When hormones trigger the macula densa cells in the DCT due to variations in blood volume, blood pressure, or electrolyte balance, these cells can immediately communicate the problem to the capillaries in the afferent and efferent arterioles, which can constrict or relax to change the glomerular filtration rate of the kidneys.

Note:
Career Connection
Nephrologist
A nephrologist studies and deals with diseases of the kidneys—both those that cause kidney failure (such as diabetes) and the conditions that are produced by kidney disease (such as hypertension). Blood pressure, blood volume, and changes in electrolyte balance come under the purview of a nephrologist.
Nephrologists usually work with other physicians who refer patients to them or consult with them about specific diagnoses and treatment plans. Patients are usually referred to a nephrologist for symptoms such as blood or protein in the urine, very high blood pressure, kidney stones, or renal failure.
Nephrology is a subspecialty of internal medicine. To become a nephrologist, medical school is followed by additional training to become certified in internal medicine. An additional two or more years is spent specifically studying kidney disorders and their accompanying effects on the body.

Section Summary

The kidneys are the main osmoregulatory organs in mammalian systems; they function to filter blood and maintain the osmolarity of body fluids at 300 mOsm. They are surrounded by three layers and are made up internally of three distinct regions—the cortex, medulla, and pelvis.

The blood vessels that transport blood into and out of the kidneys arise from and merge with the aorta and inferior vena cava, respectively. The renal arteries branch out from the aorta and enter the kidney where they further divide into segmental, interlobar, arcuate, and cortical radiate arteries.

The nephron is the functional unit of the kidney, which actively filters blood and generates urine. The nephron is made up of the renal corpuscle and renal tubule. Cortical nephrons are found in the renal cortex, while juxtamedullary nephrons are found in the renal cortex close to the renal medulla. The nephron filters and exchanges water and solutes with two sets of blood vessels and the tissue fluid in the kidneys.

There are three steps in the formation of urine: glomerular filtration, which occurs in the glomerulus; tubular reabsorption, which occurs in the renal tubules; and tubular secretion, which also occurs in the renal tubules.

Art Connections

Exercise:

Problem:

[link] Which of the following statements about the kidney is false?

    a. The renal pelvis drains into the ureter.
    b. The renal pyramids are in the medulla.
    c. The cortex covers the capsule.
    d. Nephrons are in the renal cortex.

Solution:

[link] C

Exercise:

Problem:

[link] Which of the following statements about the nephron is false?

a. The collecting duct empties into the distal convoluted tubule.
b. The Bowman's capsule surrounds the glomerulus.
c. The loop of Henle is between the proximal and distal convoluted tubules.
d. The loop of Henle empties into the distal convoluted tubule.

Solution:

[link] A

Exercise:

Problem:

[link] Loop diuretics are drugs sometimes used to treat hypertension. These drugs inhibit the reabsorption of Na^+ and Cl^- ions by the ascending limb of the loop of Henle. A side effect is that they increase urination. Why do you think this is the case?

Solution:

[link] Loop diuretics decrease the excretion of salt into the renal medulla, thereby reducing its osmolality. As a result, less water is excreted into the medulla by the descending limb, and more water is excreted as urine.

Review Questions

Exercise:

Problem: The macula densa is/are:

a. present in the renal medulla.
b. dense tissue present in the outer layer of the kidney.
c. cells present in the DCT and collecting tubules.
d. present in blood capillaries.

Solution:

C

Exercise:

Problem: The osmolarity of body fluids is maintained at _____.

    a. 100 mOsm
    b. 300 mOsm
    c. 1000 mOsm
    d. it is not constantly maintained

Solution:

B

Exercise:

Problem:

The gland located at the top of the kidney is the _____ gland.

    a. adrenal
    b. pituitary
    c. thyroid
    d. thymus

Solution:

A

Free Response

Exercise:

Problem:

Why are the loop of Henle and vasa recta important for the formation of concentrated urine?

Solution:

The loop of Henle is part of the renal tubule that loops into the renal medulla. In the loop of Henle, the filtrate exchanges solutes and water with the renal medulla and the vasa recta (the peritubular capillary network). The vasa recta acts as the countercurrent exchanger. The kidneys maintain the osmolality of the rest of the body at a constant 300 mOsm by concentrating the filtrate as it passes through the loop of Henle.

Exercise:

Problem: Describe the structure of the kidney.

Solution:

Externally, the kidneys are surrounded by three layers. The outermost layer is a tough connective tissue layer called the renal fascia. The second layer is called the perirenal fat capsule, which helps anchor the kidneys in place. The third and innermost layer is the renal capsule. Internally, the kidney has three regions—an outer cortex, a medulla in the middle, and the renal pelvis in the region called the hilum of the kidney, which is the concave part of the "bean" shape.

Glossary

afferent arteriole
    arteriole that branches from the cortical radiate artery and enters the glomerulus

arcuate artery

artery that branches from the interlobar artery and arches over the base of the renal pyramids

ascending limb
    part of the loop of Henle that ascends from the renal medulla to the renal cortex

Bowman's capsule
    structure that encloses the glomerulus

calyx
    structure that connects the renal pelvis to the renal medulla

cortex (animal)
    outer layer of an organ like the kidney or adrenal gland

cortical nephron
    nephron that lies in the renal cortex

cortical radiate artery
    artery that radiates from the arcuate arteries into the renal cortex

countercurrent exchanger
    peritubular capillary network that allows exchange of solutes and water from the renal tubules

countercurrent multiplier
    osmotic gradient in the renal medulla that is responsible for concentration of urine

descending limb
    part of the loop of Henle that descends from the renal cortex into the renal medulla

distal convoluted tubule (DCT)
    part of the renal tubule that is the most distant from the glomerulus

efferent arteriole
    arteriole that exits from the glomerulus

glomerular filtration
   filtration of blood in the glomerular capillary network into the
   glomerulus

glomerular filtration rate (GFR)
   amount of filtrate formed by the glomerulus per minute

glomerulus (renal)
   part of the renal corpuscle that contains the capillary network

hilum
   region in the renal pelvis where blood vessels, nerves, and ureters
   bunch before entering or exiting the kidney

inferior vena cava
   one of the main veins in the human body

interlobar artery
   artery that branches from the segmental artery and travels in between
   the renal lobes

juxtaglomerular cell
   cell in the afferent and efferent arterioles that responds to stimuli from
   the macula densa

juxtamedullary nephron
   nephron that lies in the cortex but close to the renal medulla

kidney
   organ that performs excretory and osmoregulatory functions

lobes of the kidney
   renal pyramid along with the adjoining cortical region

loop of Henle
   part of the renal tubule that loops into the renal medulla

macula densa

group of cells that senses changes in sodium ion concentration; present in parts of the renal tubule and collecting ducts

medulla
    middle layer of an organ like the kidney or adrenal gland

nephron
    functional unit of the kidney

perirenal fat capsule
    fat layer that suspends the kidneys

peritubular capillary network
    capillary network that surrounds the renal tubule after the efferent artery exits the glomerulus

proximal convoluted tubule (PCT)
    part of the renal tubule that lies close to the glomerulus

renal artery
    branch of the artery that enters the kidney

renal capsule
    layer that encapsulates the kidneys

renal column
    area of the kidney through which the interlobar arteries travel in the process of supplying blood to the renal lobes

renal corpuscle
    glomerulus and the Bowman's capsule together

renal fascia
    connective tissue that supports the kidneys

renal pelvis
    region in the kidney where the calyces join the ureters

renal pyramid

conical structure in the renal medulla

renal tubule
    tubule of the nephron that arises from the glomerulus

renal vein
    branch of a vein that exits the kidney and joins the inferior vena cava

segmental artery
    artery that branches from the renal artery

transport maximum
    maximum amount of solute that can be transported out of the renal
    tubules during reabsorption

tubular reabsorption
    reclamation of water and solutes that got filtered out in the glomerulus

tubular secretion
    process of secretion of wastes that do not get reabsorbed

ureter
    urine-bearing tube coming out of the kidney; carries urine to the
    bladder

urinary bladder
    structure that the ureters empty the urine into; stores urine

urine
    filtrate produced by kidneys that gets excreted out of the body

vasa recta
    peritubular network that surrounds the loop of Henle of the
    juxtamedullary nephrons

Excretion Systems
By the end of this section, you will be able to:

- Explain how vacuoles, present in microorganisms, work to excrete waste
- Describe the way in which flame cells and nephridia in worms perform excretory functions and maintain osmotic balance
- Explain how insects use Malpighian tubules to excrete wastes and maintain osmotic balance

Microorganisms and invertebrate animals use more primitive and simple mechanisms to get rid of their metabolic wastes than the mammalian system of kidney and urinary function. Three excretory systems evolved in organisms before complex kidneys: vacuoles, flame cells, and Malpighian tubules.

Contractile Vacuoles in Microorganisms

The most fundamental feature of life is the presence of a cell. In other words, a cell is the simplest functional unit of a life. Bacteria are unicellular, prokaryotic organisms that have some of the least complex life processes in place; however, prokaryotes such as bacteria do not contain membrane-bound vacuoles. The cells of microorganisms like bacteria, protozoa, and fungi are bound by cell membranes and use them to interact with the environment. Some cells, including some leucocytes in humans, are able to engulf food by endocytosis—the formation of vesicles by involution of the cell membrane within the cells. The same vesicles are able to interact and exchange metabolites with the intracellular environment. In some unicellular eukaryotic organisms such as the amoeba, shown in [link], cellular wastes and excess water are excreted by exocytosis, when the contractile vacuoles merge with the cell membrane and expel wastes into the environment. Contractile vacuoles (CV) should not be confused with vacuoles, which store food or water.
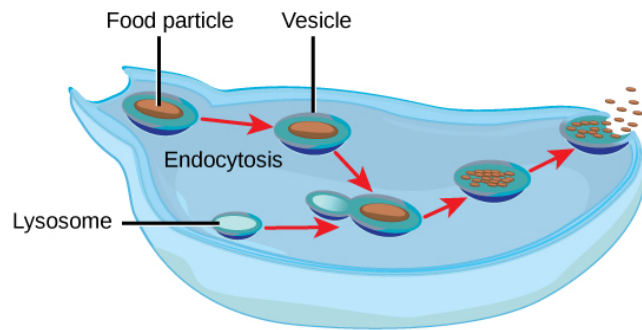
Some unicellular organisms, such as the amoeba, ingest food by endocytosis. The food vesicle fuses with a lysosome, which digests the food. Waste is excreted by exocytosis.

Flame Cells of Planaria and Nephridia of Worms

As multi-cellular systems evolved to have organ systems that divided the metabolic needs of the body, individual organs evolved to perform the excretory function. Planaria are flatworms that live in fresh water. Their excretory system consists of two tubules connected to a highly branched duct system. The cells in the tubules are called **flame cells** (or **protonephridia**) because they have a cluster of cilia that looks like a flickering flame when viewed under the microscope, as illustrated in [link]**a**. The cilia propel waste matter down the tubules and out of the body through excretory pores that open on the body surface; cilia also draw water from the interstitial fluid, allowing for filtration. Any valuable metabolites are recovered by reabsorption. Flame cells are found in flatworms, including parasitic tapeworms and free-living planaria. They also maintain the organism's osmotic balance.
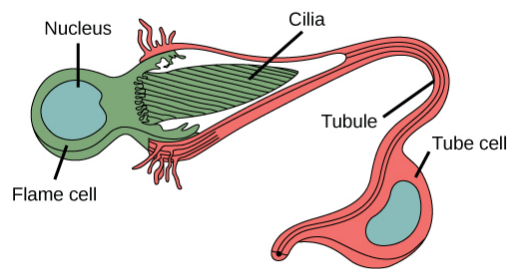
(a) Flame cell of a planarian   (b) Nephridium of an earthworm
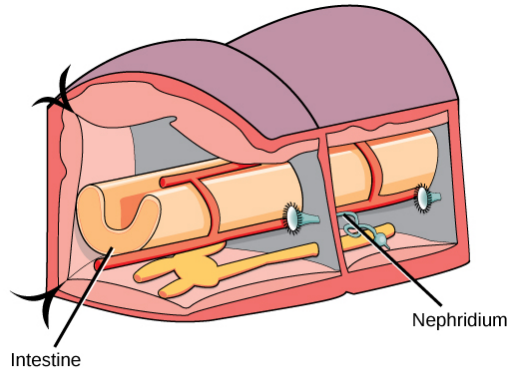
In the excretory system of the (a) planaria, cilia of flame cells propel waste through a tubule formed by a tube cell. Tubules are connected into branched structures that lead to pores located all along the sides of the body. The filtrate is secreted through these pores. In (b) annelids such as earthworms, nephridia filter fluid from the coelom, or body cavity. Beating cilia at the opening of the nephridium draw water from the coelom into a tubule. As the filtrate passes down the tubules, nutrients and other solutes are reabsorbed by capillaries. Filtered fluid containing nitrogenous and other wastes is stored in a bladder and then secreted through a pore in the side of the body.

Earthworms (annelids) have slightly more evolved excretory structures called **nephridia**, illustrated in [link]**b**. A pair of nephridia is present on each segment of the earthworm. They are similar to flame cells in that they have a tubule with cilia. Excretion occurs through a pore called the **nephridiopore**. They are more evolved than the flame cells in that they have a system for tubular reabsorption by a capillary network before excretion.

Malpighian Tubules of Insects

Malpighian tubules are found lining the gut of some species of arthropods, such as the bee illustrated in [link]. They are usually found in pairs and the

number of tubules varies with the species of insect. Malpighian tubules are convoluted, which increases their surface area, and they are lined with **microvilli** for reabsorption and maintenance of osmotic balance. Malpighian tubules work cooperatively with specialized glands in the wall of the rectum. Body fluids are not filtered as in the case of nephridia; urine is produced by tubular secretion mechanisms by the cells lining the Malpighian tubules that are bathed in hemolymph (a mixture of blood and interstitial fluid that is found in insects and other arthropods as well as most mollusks). Metabolic wastes like uric acid freely diffuse into the tubules. There are exchange pumps lining the tubules, which actively transport H^+ ions into the cell and K^+ or Na^+ ions out; water passively follows to form urine. The secretion of ions alters the osmotic pressure which draws water, electrolytes, and nitrogenous waste (uric acid) into the tubules. Water and electrolytes are reabsorbed when these organisms are faced with low-water environments, and uric acid is excreted as a thick paste or powder. Not dissolving wastes in water helps these organisms to conserve water; this is especially important for life in dry environments.
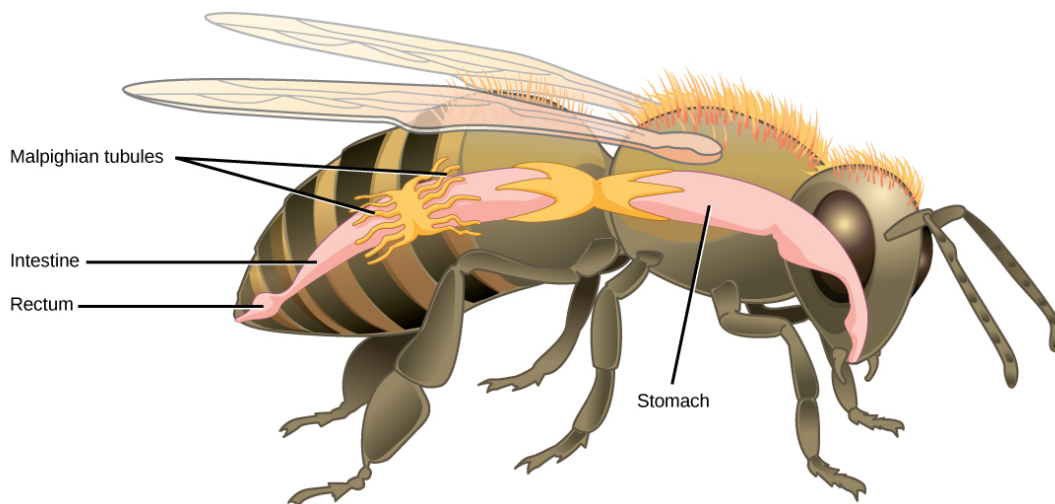
Malpighian tubules of insects and other terrestrial arthropods remove nitrogenous wastes and other solutes from the hemolymph. Na^+ and/or K^+ ions are actively transported into the lumen of the tubules. Water then enters the tubules via osmosis, forming urine. The urine passes through the intestine,

and into the rectum. There, nutrients diffuse back into the hemolymph. Na$^+$ and/or K$^+$ ions are pumped into the hemolymph, and water follows. The concentrated waste is then excreted.

Section Summary

Many systems have evolved for excreting wastes that are simpler than the kidney and urinary systems of vertebrate animals. The simplest system is that of contractile vacuoles present in microorganisms. Flame cells and nephridia in worms perform excretory functions and maintain osmotic balance. Some insects have evolved Malpighian tubules to excrete wastes and maintain osmotic balance.

Review Questions

Exercise:

   Problem: Active transport of K$^+$ in Malpighian tubules ensures that:

a. water follows K^+ to make urine
b. osmotic balance is maintained between waste matter and bodily fluids
c. both a and b
d. neither a nor b

Solution:

C

Exercise:

Problem: Contractile vacuoles in microorganisms:

a. exclusively perform an excretory function
b. can perform many functions, one of which is excretion of metabolic wastes
c. originate from the cell membrane
d. both b and c

Solution:

D

Exercise:

Problem:

Flame cells are primitive excretory organs found in _____.

a. arthropods
b. annelids
c. mammals
d. flatworms

Solution:

D

Free Response

Exercise:

Problem:

Why might specialized organs have evolved for excretion of wastes?

Solution:

The removal of wastes, which could otherwise be toxic to an organism, is extremely important for survival. Having organs that specialize in this process and that operate separately from other organs provides a measure of safety for the organism.

Exercise:

Problem:

Explain two different excretory systems other than the kidneys.

Solution:

(1) Microorganisms engulf food by endocytosis—the formation of vacuoles by involution of the cell membrane within the cells. The same vacuoles interact and exchange metabolites with the intracellular environment. Cellular wastes are excreted by exocytosis when the vacuoles merge with the cell membrane and excrete wastes into the environment. (2) Flatworms have an excretory system that consists of two tubules. The cells in the tubules are called flame cells; they have a cluster of cilia that propel waste matter down the tubules and out of the body. (3) Annelids have nephridia which have a tubule with cilia. Excretion occurs through a pore called the nephridiopore. Annelids have a system for tubular reabsorption by a capillary network before excretion. (4) Malpighian tubules are found in some species of arthropods. They are usually found in pairs, and the number of tubules varies with the species of insect. Malpighian tubules are convoluted,

which increases their surface area, and they are lined with microvilli for reabsorption and maintenance of osmotic balance. Metabolic wastes like uric acid freely diffuse into the tubules. Potassium ion pumps line the tubules, which actively transport out K^+ ions, and water follows to form urine. Water and electrolytes are reabsorbed when these organisms are faced with low-water environments, and uric acid is excreted as a thick paste or powder. By not dissolving wastes in water, these organisms conserve water.

Glossary

flame cell
    (also, protonephridia) excretory cell found in flatworms

Malpighian tubule
    excretory tubules found in arthropods

microvilli
    cellular processes that increase the surface area of cells

nephridia
    excretory structures found in annelids

nephridiopore
    pore found at the end of nephridia

Nitrogenous Wastes
By the end of this section, you will be able to:

- Compare and contrast the way in which aquatic animals and terrestrial animals can eliminate toxic ammonia from their systems
- Compare the major byproduct of ammonia metabolism in vertebrate animals to that of birds, insects, and reptiles

Of the four major macromolecules in biological systems, both proteins and nucleic acids contain nitrogen. During the catabolism, or breakdown, of nitrogen-containing macromolecules, carbon, hydrogen, and oxygen are extracted and stored in the form of carbohydrates and fats. Excess nitrogen is excreted from the body. Nitrogenous wastes tend to form toxic **ammonia**, which raises the pH of body fluids. The formation of ammonia itself requires energy in the form of ATP and large quantities of water to dilute it out of a biological system. Animals that live in aquatic environments tend to release ammonia into the water. Animals that excrete ammonia are said to be **ammonotelic**. Terrestrial organisms have evolved other mechanisms to excrete nitrogenous wastes. The animals must detoxify ammonia by converting it into a relatively nontoxic form such as urea or uric acid. Mammals, including humans, produce urea, whereas reptiles and many terrestrial invertebrates produce uric acid. Animals that secrete urea as the primary nitrogenous waste material are called **ureotelic** animals.

Nitrogenous Waste in Terrestrial Animals: The Urea Cycle

The **urea cycle** is the primary mechanism by which mammals convert ammonia to urea. Urea is made in the liver and excreted in urine. The overall chemical reaction by which ammonia is converted to urea is 2 NH_3 (ammonia) + CO_2 + 3 ATP + H_2O → H_2N-CO-NH_2 (urea) + 2 ADP + 4 P_i + AMP.

The urea cycle utilizes five intermediate steps, catalyzed by five different enzymes, to convert ammonia to urea, as shown in [link]. The amino acid L-ornithine gets converted into different intermediates before being regenerated at the end of the urea cycle. Hence, the urea cycle is also referred to as the ornithine cycle. The enzyme ornithine transcarbamylase

catalyzes a key step in the urea cycle and its deficiency can lead to accumulation of toxic levels of ammonia in the body. The first two reactions occur in the mitochondria and the last three reactions occur in the cytosol. Urea concentration in the blood, called **blood urea nitrogen** or BUN, is used as an indicator of kidney function.
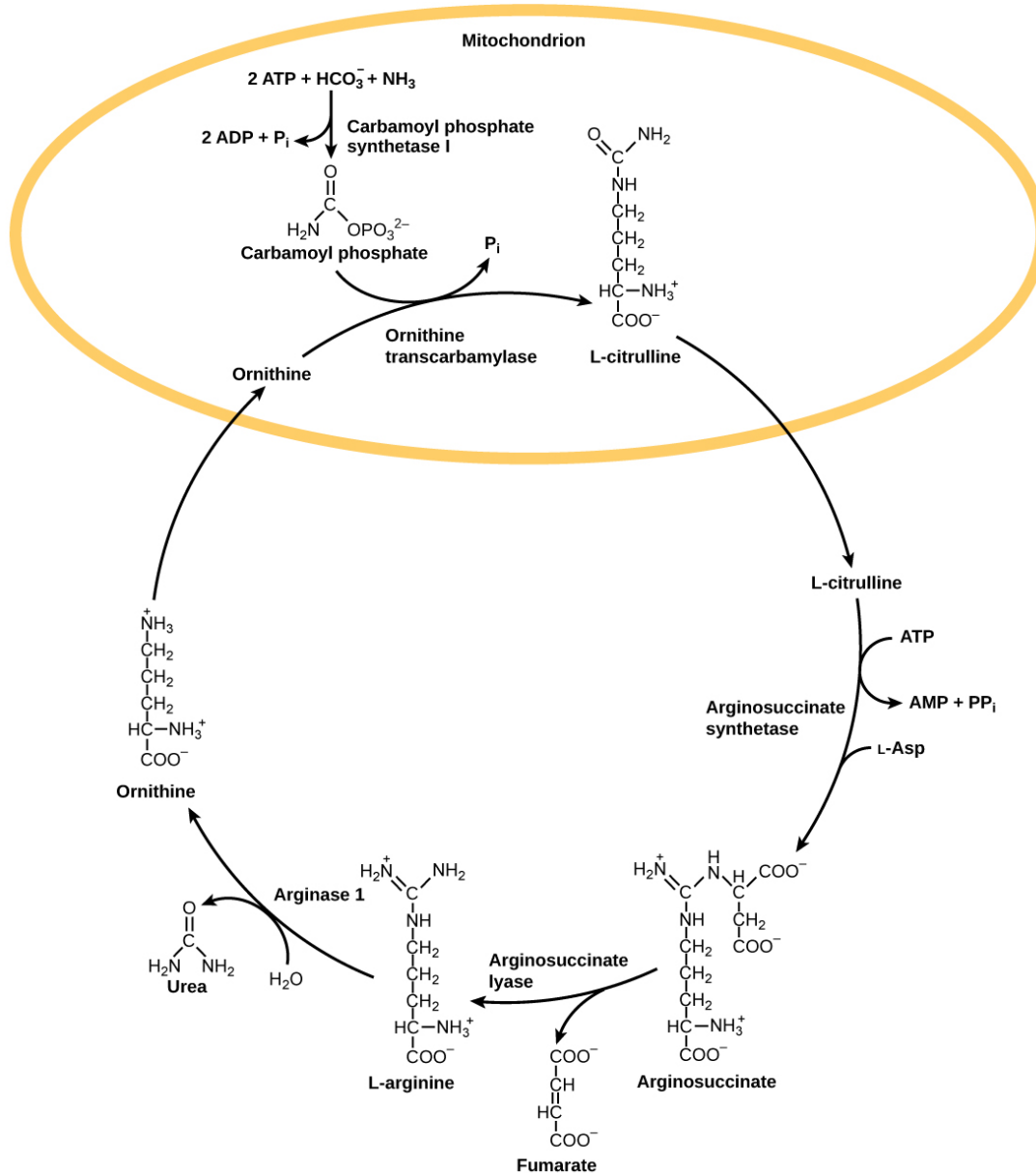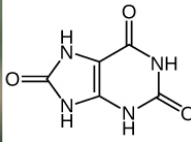
The urea cycle converts ammonia to urea.

Nitrogenous Waste in Birds and Reptiles: Uric Acid

Birds, reptiles, and most terrestrial arthropods convert toxic ammonia to **uric acid** or the closely related compound guanine (guano) instead of urea. Mammals also form some uric acid during breakdown of nucleic acids. Uric acid is a compound similar to purines found in nucleic acids. It is water insoluble and tends to form a white paste or powder; it is excreted by birds, insects, and reptiles. Conversion of ammonia to uric acid requires more energy and is much more complex than conversion of ammonia to urea [link].

(a) Many invertebrates and aquatic species excrete ammonia.

(b) Mammals, many adult amphibians, and some marine species excrete urea.

(c) Insects, land snails, birds, and many reptiles excrete uric acid.

Nitrogenous waste is excreted in different forms by different species. These include (a) ammonia, (b) urea, and (c) uric acid. (credit a: modification of work by Eric Engbretson, USFWS;

credit b: modification of work by B. "Moose" Peterson, USFWS;
credit c: modification of work by Dave Menke, USFWS)

Note:
Everyday Connection
Gout
Mammals use uric acid crystals as an **antioxidant** in their cells. However, too much uric acid tends to form kidney stones and may also cause a painful condition called gout, where uric acid crystals accumulate in the joints, as illustrated in [link]. Food choices that reduce the amount of nitrogenous bases in the diet help reduce the risk of gout. For example, tea, coffee, and chocolate have purine-like compounds, called xanthines, and should be avoided by people with gout and kidney stones.

Gout causes the inflammation visible in this person's left big toe joint. (credit: "Gonzosft"/Wikimedia Commons)

Section Summary

Ammonia is the waste produced by metabolism of nitrogen-containing compounds like proteins and nucleic acids. While aquatic animals can easily excrete ammonia into their watery surroundings, terrestrial animals have evolved special mechanisms to eliminate the toxic ammonia from their systems. Urea is the major byproduct of ammonia metabolism in vertebrate animals. Uric acid is the major byproduct of ammonia metabolism in birds, terrestrial arthropods, and reptiles.

Review Questions

Exercise:

Problem: BUN is _____.

   a. blood urea nitrogen
   b. blood uric acid nitrogen
   c. an indicator of blood volume
   d. an indicator of blood pressure

Solution:

A

Exercise:

Problem:

Human beings accumulate _____ before excreting nitrogenous waste.

   a. nitrogen
   b. ammonia
   c. urea
   d. uric acid

Solution:

C

Free Response

Exercise:

Problem:

In terms of evolution, why might the urea cycle have evolved in organisms?

Solution:

It is believed that the urea cycle evolved to adapt to a changing environment when terrestrial life forms evolved. Arid conditions probably led to the evolution of the uric acid pathway as a means of conserving water.

Exercise:

Problem:Compare and contrast the formation of urea and uric acid.

Solution:

The urea cycle is the primary mechanism by which mammals convert ammonia to urea. Urea is made in the liver and excreted in urine. The urea cycle utilizes five intermediate steps, catalyzed by five different enzymes, to convert ammonia to urea. Birds, reptiles, and insects, on the other hand, convert toxic ammonia to uric acid instead of urea. Conversion of ammonia to uric acid requires more energy and is much more complex than conversion of ammonia to urea.

Glossary

ammonia

compound made of one nitrogen atom and three hydrogen atoms

ammonotelic
describes an animal that excretes ammonia as the primary waste material

antioxidant
agent that prevents cell destruction by reactive oxygen species

blood urea nitrogen (BUN)
estimate of urea in the blood and an indicator of kidney function

urea cycle
pathway by which ammonia is converted to urea

ureotelic
describes animals that secrete urea as the primary nitrogenous waste material

uric acid
byproduct of ammonia metabolism in birds, insects, and reptiles

Hormonal Control of Osmoregulatory Functions
By the end of this section, you will be able to:

- Explain how hormonal cues help the kidneys synchronize the osmotic needs of the body
- Describe how hormones like epinephrine, norepinephrine, renin-angiotensin, aldosterone, anti-diuretic hormone, and atrial natriuretic peptide help regulate waste elimination, maintain correct osmolarity, and perform other osmoregulatory functions

While the kidneys operate to maintain osmotic balance and blood pressure in the body, they also act in concert with hormones. Hormones are small molecules that act as messengers within the body. Hormones are typically secreted from one cell and travel in the bloodstream to affect a target cell in another portion of the body. Different regions of the nephron bear specialized cells that have receptors to respond to chemical messengers and hormones. [link] summarizes the hormones that control the osmoregulatory functions.

Hormones That Affect Osmoregulation		
Hormone	**Where produced**	**Function**
Epinephrine and Norepinephrine	Adrenal medulla	Can decrease kidney function temporarily by vasoconstriction
Renin	Kidney nephrons	Increases blood pressure by acting on angiotensinogen

Hormones That Affect Osmoregulation		
Hormone	**Where produced**	**Function**
Angiotensin	Liver	Angiotensin II affects multiple processes and increases blood pressure
Aldosterone	Adrenal cortex	Prevents loss of sodium and water
Anti-diuretic hormone (vasopressin)	Hypothalamus (stored in the posterior pituitary)	Prevents water loss
Atrial natriuretic peptide	Heart atrium	Decreases blood pressure by acting as a vasodilator and increasing glomerular filtration rate; decreases sodium reabsorption in kidneys

Epinephrine and Norepinephrine

Epinephrine and norepinephrine are released by the adrenal medulla and nervous system respectively. They are the flight/fight hormones that are released when the body is under extreme stress. During stress, much of the body's energy is used to combat imminent danger. Kidney function is halted temporarily by epinephrine and norepinephrine. These hormones function by acting directly on the smooth muscles of blood vessels to constrict them. Once the afferent arterioles are constricted, blood flow into the nephrons stops. These hormones go one step further and trigger the **renin-angiotensin-aldosterone** system.

Renin-Angiotensin-Aldosterone

The renin-angiotensin-aldosterone system, illustrated in [link] proceeds through several steps to produce **angiotensin II**, which acts to stabilize blood pressure and volume. Renin (secreted by a part of the juxtaglomerular complex) is produced by the granular cells of the afferent and efferent arterioles. Thus, the kidneys control blood pressure and volume directly. Renin acts on angiotensinogen, which is made in the liver and converts it to **angiotensin I**. **Angiotensin converting enzyme (ACE)** converts angiotensin I to angiotensin II. Angiotensin II raises blood pressure by constricting blood vessels. It also triggers the release of the mineralocorticoid aldosterone from the adrenal cortex, which in turn stimulates the renal tubules to reabsorb more sodium. Angiotensin II also triggers the release of **anti-diuretic hormone (ADH)** from the hypothalamus, leading to water retention in the kidneys. It acts directly on the nephrons and decreases glomerular filtration rate. Medically, blood pressure can be controlled by drugs that inhibit ACE (called ACE inhibitors).
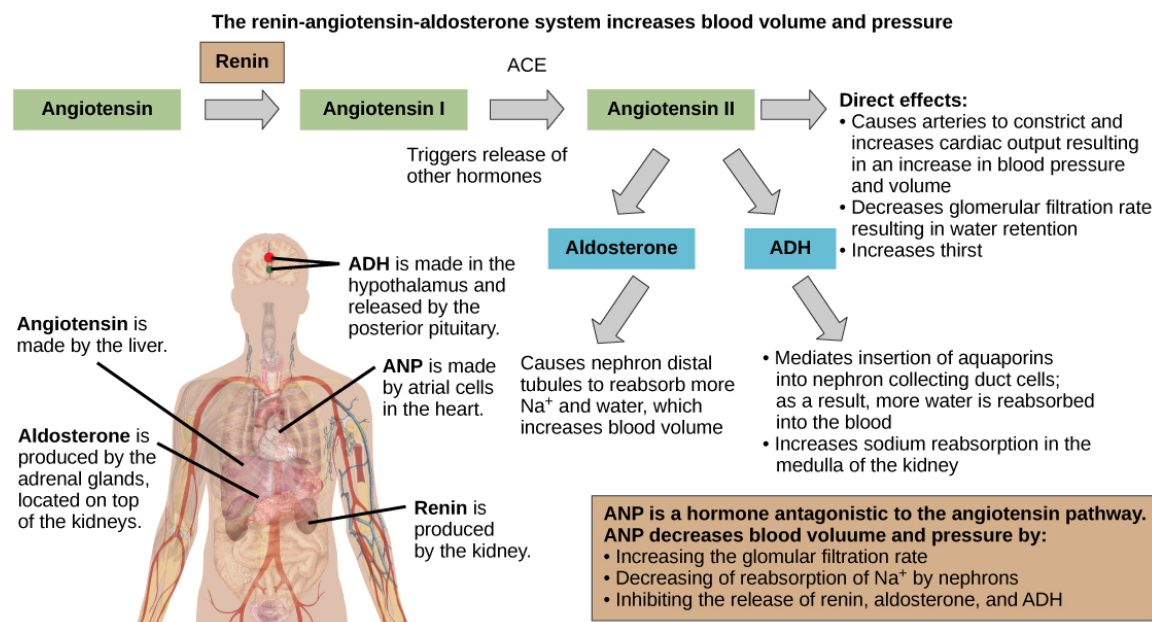
The renin-angiotensin-aldosterone system increases blood pressure and volume. The hormone ANP has antagonistic effects.

Mineralocorticoids

Mineralocorticoids are hormones synthesized by the adrenal cortex that affect osmotic balance. Aldosterone is a mineralocorticoid that regulates sodium levels in the blood. Almost all of the sodium in the blood is reclaimed by the renal tubules under the influence of aldosterone. Because sodium is always reabsorbed by active transport and water follows sodium to maintain osmotic balance, aldosterone manages not only sodium levels but also the water levels in body fluids. In contrast, the aldosterone also stimulates potassium secretion concurrently with sodium reabsorption. In contrast, absence of aldosterone means that no sodium gets reabsorbed in the renal tubules and all of it gets excreted in the urine. In addition, the daily dietary potassium load is not secreted and the retention of K^+ can cause a dangerous increase in plasma K^+ concentration. Patients who have Addison's disease have a failing adrenal cortex and cannot produce aldosterone. They lose sodium in their urine constantly, and if the supply is not replenished, the consequences can be fatal.

Antidiurectic Hormone

As previously discussed, antidiuretic hormone or ADH (also called **vasopressin**), as the name suggests, helps the body conserve water when body fluid volume, especially that of blood, is low. It is formed by the hypothalamus and is stored and released from the posterior pituitary. It acts by inserting aquaporins in the collecting ducts and promotes reabsorption of water. ADH also acts as a vasoconstrictor and increases blood pressure during hemorrhaging.

Atrial Natriuretic Peptide Hormone

The atrial natriuretic peptide (ANP) lowers blood pressure by acting as a **vasodilator**. It is released by cells in the atrium of the heart in response to

high blood pressure and in patients with sleep apnea. ANP affects salt release, and because water passively follows salt to maintain osmotic balance, it also has a diuretic effect. ANP also prevents sodium reabsorption by the renal tubules, decreasing water reabsorption (thus acting as a diuretic) and lowering blood pressure. Its actions suppress the actions of aldosterone, ADH, and renin.

Section Summary

Hormonal cues help the kidneys synchronize the osmotic needs of the body. Hormones like epinephrine, norepinephrine, renin-angiotensin, aldosterone, anti-diuretic hormone, and atrial natriuretic peptide help regulate the needs of the body as well as the communication between the different organ systems.

Review Questions

Exercise:

Problem: Renin is made by _____.

    a. granular cells of the juxtaglomerular apparatus
    b. the kidneys
    c. the nephrons
    d. All of the above.

Solution:

A

Exercise:

Problem: Patients with Addison's disease _____.

    a. retain water
    b. retain salts

c. lose salts and water
d. have too much aldosterone

Solution:

C

Exercise:

Problem: Which hormone elicits the "fight or flight" response?

a. epinephrine
b. mineralcorticoids
c. anti-diuretic hormone
d. thyroxine

Solution:

A

Free Response

Exercise:

Problem:

Describe how hormones regulate blood pressure, blood volume, and kidney function.

Solution:

Hormones are small molecules that act as messengers within the body. Different regions of the nephron bear specialized cells, which have receptors to respond to chemical messengers and hormones. The hormones carry messages to the kidney. These hormonal cues help the kidneys synchronize the osmotic needs of the body. Hormones like

epinephrine, norepinephrine, renin-angiotensin, aldosterone, anti-diuretic hormone, and atrial natriuretic peptide help regulate the needs of the body as well as the communication between the different organ systems.

Exercise:

Problem:

How does the renin-angiotensin-aldosterone mechanism function? Why is it controlled by the kidneys?

Solution:

The renin-angiotensin-aldosterone system acts through several steps to produce angiotensin II, which acts to stabilize blood pressure and volume. Thus, the kidneys control blood pressure and volume directly. Renin acts on angiotensinogen, which is made in the liver and converts it to angiotensin I. ACE (angiotensin converting enzyme) converts angiotensin I to angiotensin II. Angiotensin II raises blood pressure by constricting blood vessels. It triggers the release of aldosterone from the adrenal cortex, which in turn stimulates the renal tubules to reabsorb more sodium. Angiotensin II also triggers the release of anti-diuretic hormone from the hypothalamus, which leads to water retention. It acts directly on the nephrons and decreases GFR.

Glossary

angiotensin converting enzyme (ACE)
    enzyme that converts angiotensin I to angiotensin II

angiotensin I
    product in the renin-angiotensin-aldosterone pathway

angiotensin II
    molecule that affects different organs to increase blood pressure

anti-diuretic hormone (ADH)

hormone that prevents the loss of water

renin-angiotensin-aldosterone
biochemical pathway that activates angiotensin II, which increases blood pressure

vasodilator
compound that increases the diameter of blood vessels

vasopressin
another name for anti-diuretic hormone

Introduction class="introduction"

The (a) deer tick carries the bacterium that produces Lyme disease in humans, often evident in (b) a symptomatic bull's eye rash. The (c) white-footed mouse is one well-known host to deer ticks carrying the Lyme disease bacterium. (credit a: modification of work by Scott Bauer, USDA ARS; credit b: modification of work by James

(a)

(b)

(c)

Why study ecology? Perhaps you are interested in learning about the natural world and how living things have adapted to the physical conditions of their environment. Or, perhaps you're a future physician seeking to understand the connection between human health and ecology.

Humans are a part of the ecological landscape, and human health is one important part of human interaction with our physical and living environment. Lyme disease, for instance, serves as one modern-day example of the connection between our health and the natural world ([link]). More formally known as Lyme borreliosis, Lyme disease is a bacterial infection that can be transmitted to humans when they are bitten by the deer tick (*Ixodes scapularis*), which is the primary vector for this disease. However, not all deer ticks carry the bacteria that will cause Lyme disease in humans, and *I. scapularis* can have other hosts besides deer. In fact, it turns out that the probability of infection depends on the type of host upon which the tick develops: a higher proportion of ticks that live on

white-footed mice carry the bacterium than do ticks that live on deer. Knowledge about the environments and population densities in which the host species is abundant would help a physician or an epidemiologist better understand how Lyme disease is transmitted and how its incidence could be reduced.

The Scope of Ecology
By the end of this section, you will be able to:

- Define ecology and the four levels of ecological research
- Describe examples of the ways in which ecology requires the integration of different scientific disciplines
- Distinguish between abiotic and biotic components of the environment
- Recognize the relationship between abiotic and biotic components of the environment

Ecology is the study of the interactions of living organisms with their environment. One core goal of ecology is to understand the distribution and abundance of living things in the physical environment. Attainment of this goal requires the integration of scientific disciplines inside and outside of biology, such as biochemistry, physiology, evolution, biodiversity, molecular biology, geology, and climatology. Some ecological research also applies aspects of chemistry and physics, and it frequently uses mathematical models.

Note:
Link to Learning

openstax COLLEGE™

Climate change can alter where organisms live, which can sometimes directly affect human health. Watch the PBS video ["Feeling the Effects of Climate Change"](#) in which researchers discover a pathogenic organism living far outside of its normal range.

Levels of Ecological Study

When a discipline such as biology is studied, it is often helpful to subdivide it into smaller, related areas. For instance, cell biologists interested in cell signaling need to understand the chemistry of the signal molecules (which are usually proteins) as well as the result of cell signaling. Ecologists interested in the factors that influence the survival of an endangered species might use mathematical models to predict how current conservation efforts affect endangered organisms. To produce a sound set of management options, a conservation biologist needs to collect accurate data, including current population size, factors affecting reproduction (like physiology and behavior), habitat requirements (such as plants and soils), and potential human influences on the endangered population and its habitat (which might be derived through studies in sociology and urban ecology). Within the discipline of ecology, researchers work at four specific levels, sometimes discretely and sometimes with overlap: organism, population, community, and ecosystem ([link]).

Organisms, Populations, and Communities: In a forest, each pine tree is an organism. Together, all the pine trees make up a population. All the plant and animal species in the forest comprise a community.

Ecosystems: This coastal ecosystem in the southeastern United States includes living organisms and the environment in which they live.

The Biosphere: Encompasses all the ecosystems on Earth.

Ecologists study within several biological levels of

organization. (credit "organisms": modification of work by "Crystl"/Flickr; credit "ecosystems": modification of work by Tom Carlisle, US Fish and Wildlife Service Headquarters; credit "biosphere": NASA)

Organismal Ecology

Researchers studying ecology at the organismal level are interested in the adaptations that enable individuals to live in specific habitats. These adaptations can be morphological, physiological, and behavioral. For instance, the Karner blue butterfly (*Lycaeides melissa samuelis*) ([link]) is considered a specialist because the females preferentially oviposit (that is, lay eggs) on wild lupine. This preferential adaptation means that the Karner blue butterfly is highly dependent on the presence of wild lupine plants for its continued survival.

The Karner blue butterfly (*Lycaeides melissa samuelis*) is a rare butterfly that lives

only in open areas with few trees or shrubs, such as pine barrens and oak savannas. It can only lay its eggs on lupine plants. (credit: modification of work by J & K Hollingsworth, USFWS)

After hatching, the larval caterpillars emerge and spend four to six weeks feeding solely on wild lupine ([link]). The caterpillars pupate (undergo metamorphosis) and emerge as butterflies after about four weeks. The adult butterflies feed on the nectar of flowers of wild lupine and other plant species. A researcher interested in studying Karner blue butterflies at the organismal level might, in addition to asking questions about egg laying, ask questions about the butterflies' preferred temperature (a physiological question) or the behavior of the caterpillars when they are at different larval stages (a behavioral question).

The wild lupine (*Lupinus perennis*) is the host plant for the Karner blue butterfly.

Population Ecology

A population is a group of interbreeding organisms that are members of the same species living in the same area at the same time. (Organisms that are all members of the same species are called **conspecifics**.) A population is identified, in part, by where it lives, and its area of population may have natural or artificial boundaries: natural boundaries might be rivers, mountains, or deserts, while examples of artificial boundaries include mowed grass, manmade structures, or roads. The study of population ecology focuses on the number of individuals in an area and how and why population size changes over time. Population ecologists are particularly interested in counting the Karner blue butterfly, for example, because it is classified as federally endangered. However, the distribution and density of this species is highly influenced by the distribution and abundance of wild lupine. Researchers might ask questions about the factors leading to the decline of wild lupine and how these affect Karner blue butterflies. For example, ecologists know that wild lupine thrives in open areas where trees and shrubs are largely absent. In natural settings, intermittent wildfires regularly remove trees and shrubs, helping to maintain the open areas that wild lupine requires. Mathematical models can be used to understand how wildfire suppression by humans has led to the decline of this important plant for the Karner blue butterfly.

Community Ecology

A biological community consists of the different species within an area, typically a three-dimensional space, and the interactions within and among

these species. Community ecologists are interested in the processes driving these interactions and their consequences. Questions about conspecific interactions often focus on competition among members of the same species for a limited resource. Ecologists also study interactions among various species; members of different species are called **heterospecifics**. Examples of heterospecific interactions include predation, parasitism, herbivory, competition, and pollination. These interactions can have regulating effects on population sizes and can impact ecological and evolutionary processes affecting diversity.

For example, Karner blue butterfly larvae form mutualistic relationships with ants. Mutualism is a form of a long-term relationship that has coevolved between two species and from which each species benefits. For mutualism to exist between individual organisms, each species must receive some benefit from the other as a consequence of the relationship. Researchers have shown that there is an increase in the probability of survival when Karner blue butterfly larvae (caterpillars) are tended by ants. This might be because the larvae spend less time in each life stage when tended by ants, which provides an advantage for the larvae. Meanwhile, the Karner blue butterfly larvae secrete a carbohydrate-rich substance that is an important energy source for the ants. Both the Karner blue larvae and the ants benefit from their interaction.

Ecosystem Ecology

Ecosystem ecology is an extension of organismal, population, and community ecology. The ecosystem is composed of all the **biotic** components (living things) in an area along with the **abiotic** components (non-living things) of that area. Some of the abiotic components include air, water, and soil. Ecosystem biologists ask questions about how nutrients and energy are stored and how they move among organisms and the surrounding atmosphere, soil, and water.

The Karner blue butterflies and the wild lupine live in an oak-pine barren habitat. This habitat is characterized by natural disturbance and nutrient-poor soils that are low in nitrogen. The availability of nutrients is an important factor in the distribution of the plants that live in this habitat.

Researchers interested in ecosystem ecology could ask questions about the importance of limited resources and the movement of resources, such as nutrients, though the biotic and abiotic portions of the ecosystem.

Note:
Career Connection
Ecologist
A career in ecology contributes to many facets of human society. Understanding ecological issues can help society meet the basic human needs of food, shelter, and health care. Ecologists can conduct their research in the laboratory and outside in natural environments ([link]). These natural environments can be as close to home as the stream running through your campus or as far away as the hydrothermal vents at the bottom of the Pacific Ocean. Ecologists manage natural resources such as white-tailed deer populations (*Odocoileus virginianus*) for hunting or aspen (*Populus* spp.) timber stands for paper production. Ecologists also work as educators who teach children and adults at various institutions including universities, high schools, museums, and nature centers. Ecologists may also work in advisory positions assisting local, state, and federal policymakers to develop laws that are ecologically sound, or they may develop those policies and legislation themselves. To become an ecologist requires an undergraduate degree, usually in a natural science. The undergraduate degree is often followed by specialized training or an advanced degree, depending on the area of ecology selected. Ecologists should also have a broad background in the physical sciences, as well as a sound foundation in mathematics and statistics.

This landscape ecologist is releasing a black-footed ferret into its native habitat as part of a study. (credit: USFWS Mountain Prairie Region, NPS)

Section Summary

Ecology is the study of the interactions of living things with their environment. Ecologists ask questions across four levels of biological organization—organismal, population, community, and ecosystem. At the organismal level, ecologists study individual organisms and how they interact with their environments. At the population and community levels, ecologists explore, respectively, how a population of organisms changes over time and the ways in which that population interacts with other species in the community. Ecologists studying an ecosystem examine the living species (the biotic components) of the ecosystem as well as the nonliving

portions (the abiotic components), such as air, water, and soil, of the environment.

Review Questions

Exercise:

Problem: Which of the following is a biotic factor?

    a. wind
    b. disease-causing microbe
    c. temperature
    d. soil particle size

Solution:

B

Exercise:

Problem:

The study of nutrient cycling though the environment is an example of which of the following?

    a. organismal ecology
    b. population ecology
    c. community ecology
    d. ecosystem ecology

Solution:

D

Free Response

Exercise:

  Problem:

  Ecologists often collaborate with other researchers interested in ecological questions. Describe the levels of ecology that would be easier for collaboration because of the similarities of questions asked. What levels of ecology might be more difficult for collaboration?

  Solution:

  Ecologists working in organismal or population ecology might ask similar questions about how the biotic and abiotic conditions affect particular organisms and, thus, might find collaboration to be mutually beneficial. Levels of ecology such as community ecology or ecosystem ecology might pose greater challenges for collaboration because these areas are very broad and may include many different environmental components.

Exercise:

  Problem:

  The population is an important unit in ecology as well as other biological sciences. How is a population defined, and what are the strengths and weaknesses of this definition? Are there some species that at certain times or places are not in populations?

  Solution:

  It is beneficial to consider a population to be all of the individuals living in the same area at the same time because it allows the ecologist to identify and study all of the abiotic and biotic factors that may affect the members of the population. However, this definition of a population could be considered a drawback if it prohibits the ecologist from studying a population's individuals that may be transitory, but still influential. Some species with members that have a wide geographic range might not be considered to be a population, but could still have many of the qualities of a population.

Glossary

abiotic
    nonliving components of the environment

biotic
    living components of the environment

conspecifics
    individuals that are members of the same species

ecology
    study of interaction between living things and their environment

heterospecifics
    individuals that are members of different species

Biogeography
By the end of this section, you will be able to:

- Define biogeography
- List and describe abiotic factors that affect the global distribution of plant and animal species
- Compare the impact of abiotic forces on aquatic and terrestrial environments
- Summarize the affect of abiotic factors on net primary productivity

Many forces influence the communities of living organisms present in different parts of the biosphere (all of the parts of Earth inhabited by life). The biosphere extends into the atmosphere (several kilometers above Earth) and into the depths of the oceans. Despite its apparent vastness to an individual human, the biosphere occupies only a minute space when compared to the known universe. Many abiotic forces influence where life can exist and the types of organisms found in different parts of the biosphere. The abiotic factors influence the distribution of **biomes**: large areas of land with similar climate, flora, and fauna.

Biogeography

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors such as temperature and rainfall vary based mainly on latitude and elevation. As these abiotic factors change, the composition of plant and animal communities also changes. For example, if you were to begin a journey at the equator and walk north, you would notice gradual changes in plant communities. At the beginning of your journey, you would see tropical wet forests with broad-leaved evergreen trees, which are characteristic of plant communities found near the equator. As you continued to travel north, you would see these broad-leaved evergreen plants eventually give rise to seasonally dry forests with scattered trees. You would also begin to notice changes in temperature and moisture. At about 30 degrees north, these forests would give way to deserts, which are characterized by low precipitation.

Moving farther north, you would see that deserts are replaced by grasslands or prairies. Eventually, grasslands are replaced by deciduous temperate forests. These deciduous forests give way to the boreal forests found in the subarctic, the area south of the Arctic Circle. Finally, you would reach the Arctic tundra, which is found at the most northern latitudes. This trek north reveals gradual changes in both climate and the types of organisms that have adapted to environmental factors associated with ecosystems found at different latitudes. However, different ecosystems exist at the same latitude due in part to abiotic factors such as jet streams, the Gulf Stream, and ocean currents. If you were to hike up a mountain, the changes you would see in the vegetation would parallel those as you move to higher latitudes.

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An **endemic** species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution; therefore, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia ([link]**ab**).

Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal. (credit a: modification of work by Derrick Coetzee; credit b: modification of work by Allan Whittome)

Sometimes ecologists discover unique patterns of species distribution by determining where species are *not* found. Hawaii, for example, has no native land species of reptiles or amphibians, and has only one native terrestrial mammal, the hoary bat. Most of New Guinea, as another example, lacks placental mammals.

Note:
Link to Learning

Check out this [video](#) to observe a platypus swimming in its natural habitat in New South Wales, Australia.

Plants can be endemic or generalists: endemic plants are found only on specific regions of the Earth, while generalists are found on many regions. Isolated land masses—such as Australia, Hawaii, and Madagascar—often have large numbers of endemic plant species. Some of these plants are endangered due to human activity. The forest gardenia (*Gardenia brighamii*), for instance, is endemic to Hawaii; only an estimated 15–20 trees are thought to exist ([link]).

Listed as federally endangered, the forest gardenia is a small tree with distinctive flowers. It is found only in five of the Hawaiian Islands in small

populations consisting of a
few individual specimens.
(credit: Forest & Kim
Starr)

Energy Sources

Energy from the sun is captured by green plants, algae, cyanobacteria, and photosynthetic protists. These organisms convert solar energy into the chemical energy needed by all living things. Light availability can be an important force directly affecting the evolution of adaptations in photosynthesizers. For instance, plants in the understory of a temperate forest are shaded when the trees above them in the canopy completely leaf out in the late spring. Not surprisingly, understory plants have adaptations to successfully capture available light. One such adaptation is the rapid growth of spring ephemeral plants such as the spring beauty ([link]). These spring flowers achieve much of their growth and finish their life cycle (reproduce) early in the season before the trees in the canopy develop leaves.

The spring beauty is an ephemeral spring plant that flowers early in the spring to avoid competing with larger forest trees for sunlight. (credit: John Beetham)

In aquatic ecosystems, the availability of light may be limited because sunlight is absorbed by water, plants, suspended particles, and resident microorganisms. Toward the bottom of a lake, pond, or ocean, there is a zone that light cannot reach. Photosynthesis cannot take place there and, as a result, a number of adaptations have evolved that enable living things to survive without light. For instance, aquatic plants have photosynthetic tissue near the surface of the water; for example, think of the broad, floating leaves of a water lily—water lilies cannot survive without light. In environments such as hydrothermal vents, some bacteria extract energy from inorganic chemicals because there is no light for photosynthesis.

The availability of nutrients in aquatic systems is also an important aspect of energy or photosynthesis. Many organisms sink to the bottom of the ocean when they die in the open water; when this occurs, the energy found in that living organism is sequestered for some time unless ocean upwelling occurs. **Ocean upwelling** is the rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline ([link]). As the wind pushes ocean waters offshore, water from the bottom of the ocean moves up to replace this water. As a result, the nutrients once contained in dead organisms become available for reuse by other living organisms.
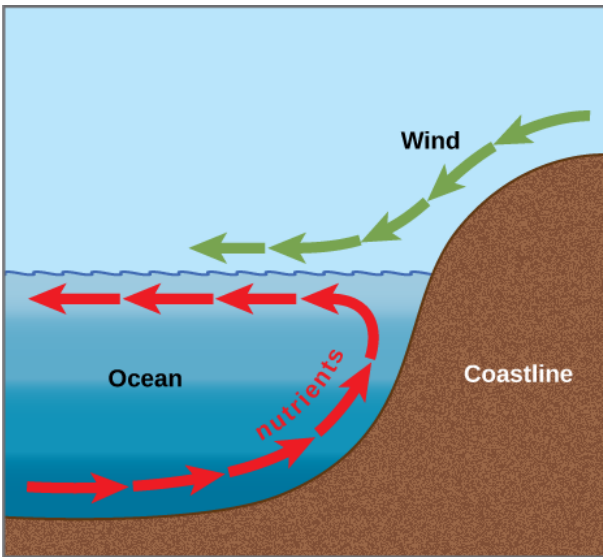
Ocean upwelling is an important process that recycles nutrients and energy in the ocean. As wind (green arrows) pushes offshore, it causes water from the ocean bottom (red arrows) to move to the surface, bringing up nutrients from the ocean depths.

In freshwater systems, the recycling of nutrients occurs in response to air temperature changes. The nutrients at the bottom of lakes are recycled twice each year: in the spring and fall turnover. The **spring and fall turnover** is a seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top of a body of water ([link]). These turnovers are caused by the formation of a **thermocline**: a layer of water with a temperature that is significantly different from that of the surrounding layers. In wintertime, the surface of lakes found in many northern regions is frozen. However, the water under the ice is slightly warmer, and the water at the bottom of the lake is warmer yet at 4 °C to 5 °C (39.2 °F to 41 °F). Water is densest at 4 °C; therefore, the deepest water is also the densest. The deepest water is oxygen poor because the decomposition of organic material at the bottom of the lake uses up available oxygen that cannot be

replaced by means of oxygen diffusion into the water due to the surface ice layer.
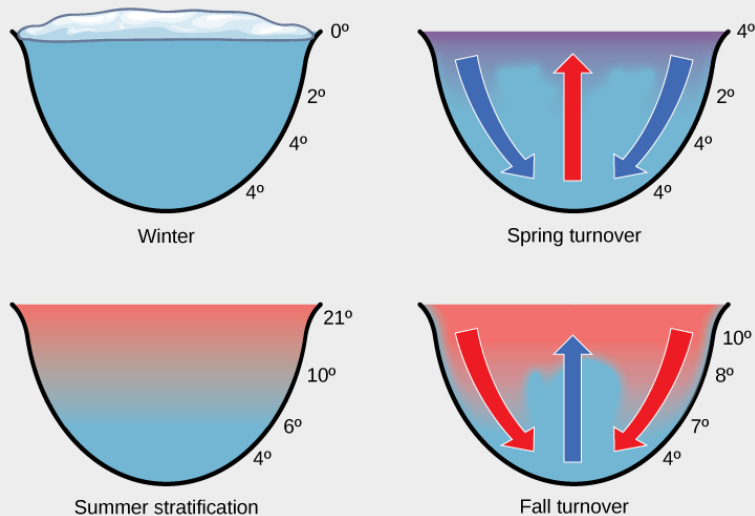
The spring and fall turnovers are important processes in freshwater lakes that act to move the nutrients and oxygen at the bottom of deep lakes to the top. Turnover occurs because water has a maximum density at 4 °C. Surface water temperature changes as the seasons progress, and denser water sinks.

How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

In springtime, air temperatures increase and surface ice melts. When the temperature of the surface water begins to reach 4 °C, the water becomes heavier and sinks to the bottom. The water at the bottom of the lake is then

displaced by the heavier surface water and, thus, rises to the top. As that water rises to the top, the sediments and nutrients from the lake bottom are brought along with it. During the summer months, the lake water stratifies, or forms layers, with the warmest water at the lake surface.

As air temperatures drop in the fall, the temperature of the lake water cools to 4 °C; therefore, this causes fall turnover as the heavy cold water sinks and displaces the water at the bottom. The oxygen-rich water at the surface of the lake then moves to the bottom of the lake, while the nutrients at the bottom of the lake rise to the surface ([link]). During the winter, the oxygen at the bottom of the lake is used by decomposers and other organisms requiring oxygen, such as fish.

Temperature

Temperature affects the physiology of living things as well as the density and state of water. Temperature exerts an important influence on living things because few living things can survive at temperatures below 0 °C (32 °F) due to metabolic constraints. It is also rare for living things to survive at temperatures exceeding 45 °C (113 °F); this is a reflection of evolutionary response to typical temperatures. Enzymes are most efficient within a narrow and specific range of temperatures; enzyme degradation can occur at higher temperatures. Therefore, organisms either must maintain an internal temperature or they must inhabit an environment that will keep the body within a temperature range that supports metabolism. Some animals have adapted to enable their bodies to survive significant temperature fluctuations, such as seen in hibernation or reptilian torpor. Similarly, some bacteria are adapted to surviving in extremely hot temperatures such as geysers. Such bacteria are examples of extremophiles: organisms that thrive in extreme environments.

Temperature can limit the distribution of living things. Animals faced with temperature fluctuations may respond with adaptations, such as migration, in order to survive. Migration, the movement from one place to another, is an adaptation found in many animals, including many that inhabit seasonally cold climates. Migration solves problems related to temperature,

locating food, and finding a mate. In migration, for instance, the Arctic Tern (*Sterna paradisaea*) makes a 40,000 km (24,000 mi) round trip flight each year between its feeding grounds in the southern hemisphere and its breeding grounds in the Arctic Ocean. Monarch butterflies (*Danaus plexippus*) live in the eastern United States in the warmer months and migrate to Mexico and the southern United States in the wintertime. Some species of mammals also make migratory forays. Reindeer (*Rangifer tarandus*) travel about 5,000 km (3,100 mi) each year to find food. Amphibians and reptiles are more limited in their distribution because they lack migratory ability. Not all animals that can migrate do so: migration carries risk and comes at a high energy cost.

Some animals hibernate or estivate to survive hostile temperatures. Hibernation enables animals to survive cold conditions, and estivation allows animals to survive the hostile conditions of a hot, dry climate. Animals that hibernate or estivate enter a state known as torpor: a condition in which their metabolic rate is significantly lowered. This enables the animal to wait until its environment better supports its survival. Some amphibians, such as the wood frog (*Rana sylvatica*), have an antifreeze-like chemical in their cells, which retains the cells' integrity and prevents them from bursting.

Water

Water is required by all living things because it is critical for cellular processes. Since terrestrial organisms lose water to the environment by simple diffusion, they have evolved many adaptations to retain water.

- Plants have a number of interesting features on their leaves, such as leaf hairs and a waxy cuticle, that serve to decrease the rate of water loss via transpiration.
- Freshwater organisms are surrounded by water and are constantly in danger of having water rush into their cells because of osmosis. Many adaptations of organisms living in freshwater environments have evolved to ensure that solute concentrations in their bodies remain

within appropriate levels. One such adaptation is the excretion of dilute urine.

- Marine organisms are surrounded by water with a higher solute concentration than the organism and, thus, are in danger of losing water to the environment because of osmosis. These organisms have morphological and physiological adaptations to retain water and release solutes into the environment. For example, Marine iguanas (*Amblyrhynchus cristatus*), sneeze out water vapor that is high in salt in order to maintain solute concentrations within an acceptable range while swimming in the ocean and eating marine plants.

Inorganic Nutrients and Soil

Inorganic nutrients, such as nitrogen and phosphorus, are important in the distribution and the abundance of living things. Plants obtain these inorganic nutrients from the soil when water moves into the plant through the roots. Therefore, soil structure (particle size of soil components), soil pH, and soil nutrient content play an important role in the distribution of plants. Animals obtain inorganic nutrients from the food they consume. Therefore, animal distributions are related to the distribution of what they eat. In some cases, animals will follow their food resource as it moves through the environment.

Other Aquatic Factors

Some abiotic factors, such as oxygen, are important in aquatic ecosystems as well as terrestrial environments. Terrestrial animals obtain oxygen from the air they breathe. Oxygen availability can be an issue for organisms living at very high elevations, however, where there are fewer molecules of oxygen in the air. In aquatic systems, the concentration of dissolved oxygen is related to water temperature and the speed at which the water moves. Cold water has more dissolved oxygen than warmer water. In addition, salinity, current, and tide can be important abiotic factors in aquatic ecosystems.

Other Terrestrial Factors

Wind can be an important abiotic factor because it influences the rate of evaporation and transpiration. The physical force of wind is also important because it can move soil, water, or other abiotic factors, as well as an ecosystem's organisms.

Fire is another terrestrial factor that can be an important agent of disturbance in terrestrial ecosystems. Some organisms are adapted to fire and, thus, require the high heat associated with fire to complete a part of their life cycle. For example, the jack pine—a coniferous tree—requires heat from fire for its seed cones to open ([link]). Through the burning of pine needles, fire adds nitrogen to the soil and limits competition by destroying undergrowth.

The mature cones of the jack pine *(Pinus banksiana)* open only when exposed to high temperatures, such as during a forest fire. A fire is likely to kill most vegetation, so a seedling that germinates after a fire is more likely to receive ample sunlight than one that germinates under normal conditions. (credit: USDA)

Abiotic Factors Influencing Plant Growth

Temperature and moisture are important influences on plant production (primary productivity) and the amount of organic matter available as food (net primary productivity). **Net primary productivity** is an estimation of all of the organic matter available as food; it is calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration. In terrestrial environments, net primary productivity is estimated by measuring the **aboveground biomass** per unit area, which is the total mass of living plants, excluding roots. This means that a large percentage of plant biomass which exists underground is not included in this measurement. Net primary productivity is an important variable when considering differences in biomes. Very productive biomes have a high level of aboveground biomass.

Annual biomass production is directly related to the abiotic components of the environment. Environments with the greatest amount of biomass have conditions in which photosynthesis, plant growth, and the resulting net primary productivity are optimized. The climate of these areas is warm and wet. Photosynthesis can proceed at a high rate, enzymes can work most efficiently, and stomata can remain open without the risk of excessive transpiration; together, these factors lead to the maximal amount of carbon dioxide (CO_2) moving into the plant, resulting in high biomass production. The aboveground biomass produces several important resources for other living things, including habitat and food. Conversely, dry and cold environments have lower photosynthetic rates and therefore less biomass. The animal communities living there will also be affected by the decrease in available food.

Section Summary

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Endemic species are species that are naturally found only in a specific geographic area. The

distribution of living things is influenced by several environmental factors that are, in part, controlled by the latitude or elevation at which an organism is found. Ocean upwelling and spring and fall turnovers are important processes regulating the distribution of nutrients and other abiotic factors important in aquatic ecosystems. Energy sources, temperature, water, inorganic nutrients, and soil are factors limiting the distribution of living things in terrestrial systems. Net primary productivity is a measure of the amount of biomass produced by a biome.

Art Connections

Exercise:

Problem:

[link] How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

Solution:

[link] Tropical lakes don't freeze, so they don't undergo spring turnover in the same way temperate lakes do. However, stratification does occur, as well as seasonal turnover.

Review Questions

Exercise:

Problem:

Understory plants in a temperate forest have adaptations to capture limited _____.

    a. water
    b. nutrients
    c. heat
    d. sunlight

Solution:

D

Exercise:

Problem:

An ecologist hiking up a mountain may notice different biomes along the way due to changes in all of the following except:

    a. elevation
    b. rainfall
    c. latitude
    d. temperature

Solution:

C

Free Response

Exercise:

Problem:

Compare and contrast ocean upwelling and spring and fall turnovers.

Solution:

Ocean upwelling is a continual process that occurs year-round. Spring and fall turnover in freshwater lakes and ponds, however, is a seasonal process that occurs due to temperature changes in the water that take place during springtime warming and autumn cooling. Both ocean upwelling and spring and fall turnover enable nutrients in the organic materials at the bottom of the body of water to be recycled and reused by living things.

Exercise:

Problem:

Many endemic species are found in areas that are geographically isolated. Suggest a plausible scientific explanation for why this is so.

Solution:

Areas that have been geographically isolated for very long periods of time allow unique species to evolve; these species are distinctly different from those of surrounding areas and remain so, since geographic isolation keeps them separated from other species.

Glossary

aboveground biomass
> total mass of aboveground living plants per area

biogeography
> study of the geographic distribution of living things and the abiotic factors that affect their distribution

biome
> ecological community of plants, animals, and other organisms that is adapted to a characteristic set of environmental conditions

endemic
> species found only in a specific geographic area that is usually restricted in size

fall and spring turnover
> seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top

net primary productivity
> measurement of the energy accumulation within an ecosystem, calculated as the total amount of carbon fixed per year minus the

amount that is oxidized during cellular respiration

ocean upwelling
    rising of deep ocean waters that occurs when prevailing winds blow
    along surface waters near a coastline

thermocline
    layer of water with a temperature that is significantly different from
    that of the surrounding layers

Terrestrial Biomes
By the end of this section, you will be able to:

- Identify the two major abiotic factors that determine terrestrial biomes
- Recognize distinguishing characteristics of each of the eight major terrestrial biomes

The Earth's biomes are categorized into two major groups: terrestrial and aquatic. Terrestrial biomes are based on land, while aquatic biomes include both ocean and freshwater biomes. The eight major terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation. Comparing the annual totals of precipitation and fluctuations in precipitation from one biome to another provides clues as to the importance of abiotic factors in the distribution of biomes. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of the biome and the vegetation type in the biome. The distribution of these biomes shows that the same biome can occur in geographically distinct areas with similar climates ([link]).

Note:
Art Connection

| Tropical forest | Savanna | Desert | Chaparral | Temperate forest |
| Boreal forest | Tundra | Mountains | Polar ice | Temperate grassland |
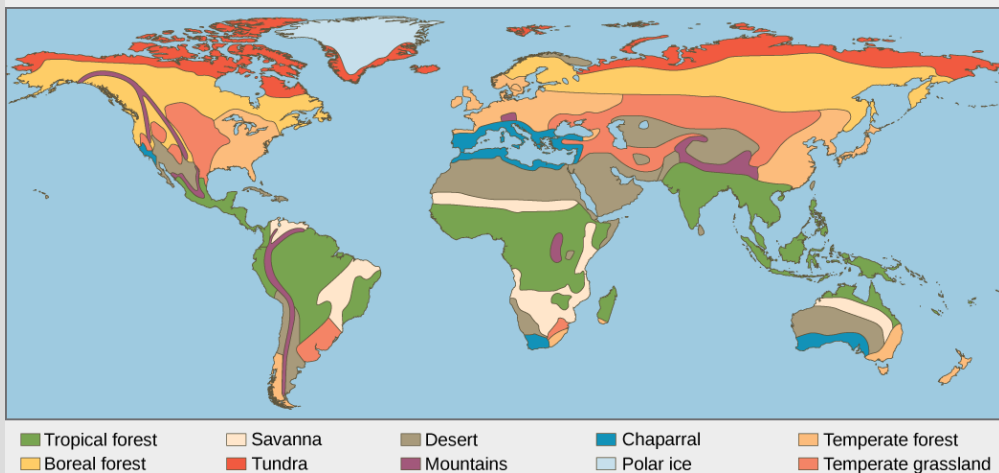
Each of the world's major biomes is distinguished by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown.

Which of the following statements about biomes is false?

  a. Chaparral is dominated by shrubs.
  b. Savannas and temperate grasslands are dominated by grasses.
  c. Boreal forests are dominated by deciduous trees.
  d. Lichens are common in the arctic tundra.

Tropical Wet Forest

Tropical wet forests are also referred to as tropical rainforests. This biome is found in equatorial regions ([link]). The vegetation is characterized by plants with broad leaves that fall off throughout the year. Unlike the trees of deciduous forests, the trees in this biome do not have a seasonal loss of leaves associated with variations in temperature and sunlight; these forests are "evergreen" year-round.

The temperature and sunlight profiles of tropical wet forests are very stable in comparison to that of other terrestrial biomes, with the temperatures ranging from 20 °C to 34 °C (68 °F to 93 °F). When one compares the annual temperature variation of tropical wet forests with that of other forest biomes, the lack of seasonal temperature variation in the tropical wet forest becomes apparent. This lack of seasonality leads to year-round plant growth, rather than the seasonal (spring, summer, and fall) growth seen in other biomes. In contrast to other ecosystems, tropical ecosystems do not have long days and short days during the yearly cycle. Instead, a constant daily amount of sunlight (11–12 hrs per day) provides more solar radiation, thereby, a longer period of time for plant growth.

The annual rainfall in tropical wet forests ranges from 125 to 660 cm (50–200 in) with some monthly variation. While sunlight and temperature remain fairly consistent, annual rainfall is highly variable. Tropical wet forests have wet months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm

(3.5 in) of rainfall. However, the driest month of a tropical wet forest still exceeds the *annual* rainfall of some other biomes, such as deserts.

Tropical wet forests have high net primary productivity because the annual temperatures and precipitation values in these areas are ideal for plant growth. Therefore, the extensive biomass present in the tropical wet forest leads to plant communities with very high species diversities ([link]). Tropical wet forests have more species of trees than any other biome; on average between 100 and 300 species of trees are present in a single hectare (2.5 acres) of South America. One way to visualize this is to compare the distinctive horizontal layers within the tropical wet forest biome. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short shrubby foliage. A layer of trees rises above this understory and is topped by a closed upper **canopy**—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, fungi, animals, and other organisms within the tropical wet forests. For instance, epiphytes are plants that grow on other plants, which typically are not harmed. Epiphytes are found throughout tropical wet forest biomes. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground and have adapted to this arboreal lifestyle.

Tropical wet forests, such as these forests of Madre de Dios, Peru, near the Amazon River, have high species diversity. (credit: Roosevelt Garcia)

Savannas

Savannas are grasslands with scattered trees, and they are located in Africa, South America, and northern Australia ([link]). Savannas are hot, tropical areas with temperatures averaging from 24 °C to 29 °C (75 °F to 84 °F) and an annual rainfall of 10–40 cm (3.9–15.7 in). Savannas have an extensive dry season; for this reason, forest trees do not grow as well as they do in the tropical wet forest (or other forest biomes). As a result, within the grasses and forbs (herbaceous flowering plants) that dominate the savanna, there are relatively few trees ([link]). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly re-sprout after a fire.

Savannas, like this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses. (credit: Christopher T. Cooper)

Subtropical Deserts

Subtropical deserts exist between 15 ° and 30 ° north and south latitude and are centered on the Tropics of Cancer and Capricorn ([link]). This biome is very dry; in some years, evaporation exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60 °C (140 °F) and nighttime temperatures approaching 0 °C (32 °F). In cold deserts, temperatures can be as high as 25 °C and can drop below -30 °C (-22 °F). Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in) with little monthly variation and lack of predictability in rainfall. In some cases, the annual rainfall can be as low as 2 cm (0.8 in) in subtropical deserts located in central Australia ("the Outback") and northern Africa.

The vegetation and low animal diversity of this biome is closely related to this low and unpredictable precipitation. Very dry deserts lack perennial vegetation that lives from one year to the next; instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, then they die. Many other plants in these areas are characterized by having a number of adaptations that conserve water, such as deep roots, reduced foliage, and water-storing stems ([link]). Seed plants in the desert produce seeds that can be in dormancy for extended periods between rains. Adaptations in desert animals include nocturnal behavior and burrowing.

To reduce water loss, many desert plants have tiny leaves or no leaves at all. The leaves of ocotillo (*Fouquieria splendens*), shown here in the Sonora Desert near Gila Bend, Arizona, appear only after rainfall, and then are shed.

Chaparral

The chaparral is also called the scrub forest and is found in California, along the Mediterranean Sea, and along the southern coast of Australia ([link]). The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in), and the majority of the rain falls in the winter. Summers are very dry and many chaparral plants are dormant during the summertime.

The chaparral vegetation, shown in [link], is dominated by shrubs and is adapted to periodic fires, with some plants producing seeds that only germinate after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote plant regrowth.

The chaparral is dominated by shrubs. (credit: Miguel Vieira)

Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as prairies; they are also in Eurasia, where they are known as steppes ([link]). Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth and when ample water is available, which occurs in the spring, summer, and fall. During much of the winter, temperatures are low, and water, which is stored in the form of ice, is not available for plant growth.

Annual precipitation ranges from 25 cm to 75 cm (9.8–29.5 in). Because of relatively lower annual precipitation in temperate grasslands, there are few

trees except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses and some prairies sustain populations of grazing animals [link]. The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and rhizomes (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay.

The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. (credit: Jack Dykinga, USDA Agricultural Research Service)

Fires, mainly caused by lightning, are a natural disturbance in temperate grasslands. When fire is suppressed in temperate grasslands, the vegetation eventually converts to scrub and dense forests. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.

Temperate Forests

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand ([link]). This biome is found throughout mid-latitude regions. Temperatures range between -30 °C and 30 °C (-22 °F to 86 °F) and drop to below freezing on an annual basis. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm (29.5–59 in).

Because of the moderate annual rainfall and temperatures, deciduous trees are the dominant plant in this biome ([link]). Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, no photosynthesis occurs in the deciduous trees during the dormant winter period. Each spring, new leaves appear as the temperature increases. Because of the dormant period, the net primary productivity of temperate forests is less than that of tropical wet forests. In addition, temperate forests show less diversity of tree species than tropical wet forest biomes.

Deciduous trees are the dominant plant in the temperate forest. (credit: Oliver Herold)

The trees of the temperate forests leaf out and shade much of the ground; however, this biome is more open than tropical wet forests because trees in the temperate forests do not grow as tall as the trees in tropical wet forests. The soils of the temperate forests are rich in inorganic and organic nutrients. This is due to the thick layer of leaf litter on forest floors. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, such as the red-backed salamander (*Plethodon cinereus*).

Boreal Forests

The boreal forest, also known as taiga or coniferous forest, is found south of the Arctic Circle and across most of Canada, Alaska, Russia, and northern Europe ([link]). This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm (15.7–39 in) and usually takes the form of snow. Little evaporation occurs because of the cold temperatures.

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the sun is required to warm a needle-like leaf than a broad leaf. This benefits evergreen trees, which grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles may have a competitive advantage over the broad-leafed deciduous trees.

The net primary productivity of boreal forests is lower than that of temperate forests and tropical wet forests. The aboveground biomass of boreal forests is high because these slow-growing tree species are long lived and accumulate standing biomass over time. Plant species diversity is less than that seen in temperate forests and tropical wet forests. Boreal forests

lack the pronounced elements of the layered forest structure seen in tropical wet forests. The structure of a boreal forest is often only a tree layer and a ground layer ([link]). When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth.

The boreal forest (taiga) has low lying plants and conifer trees. (credit: L.B. Brubaker)

Arctic Tundra

The Arctic tundra lies north of the subarctic boreal forest and is located throughout the Arctic regions of the northern hemisphere ([link]). The average winter temperature is -34 °C (-34 °F) and the average summer temperature is from 3 °C to 12 °C (37 °F–52 °F). Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks. However, during this time, there are almost 24 hours of daylight and plant growth is rapid. The annual precipitation of the Arctic tundra is very low with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation due to the cold temperatures.

Plants in the Arctic tundra are generally low to the ground ([link]). There is little species diversity, low net primary productivity, and low aboveground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as **permafrost**. The permafrost makes it impossible for roots to penetrate deep into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.

Low-growing plants such as shrub willow dominate the tundra landscape, shown here in the Arctic National Wildlife Refuge. (credit: USFWS Arctic National Wildlife Refuge)

Note:
Link to Learning

Watch this *Assignment Discovery: Biomes* video for an overview of biomes. To explore further, select one of the biomes on the extended playlist: desert, savanna, temperate forest, temperate grassland, tropic, tundra.

Section Summary

The Earth has terrestrial biomes and aquatic biomes. Aquatic biomes include both freshwater and marine environments. There are eight major terrestrial biomes: tropical wet forests, savannas, subtropical deserts, chaparral, temperate grasslands, temperate forests, boreal forests, and Arctic tundra. The same biome can occur in different geographic locations with similar climates. Temperature and precipitation, and variations in both, are key abiotic factors that shape the composition of animal and plant communities in terrestrial biomes. Some biomes, such as temperate grasslands and temperate forests, have distinct seasons, with cold weather and hot weather alternating throughout the year. In warm, moist biomes, such as the tropical wet forest, net primary productivity is high, as warm temperatures, abundant water, and a year-round growing season fuel plant growth. Other biomes, such as deserts and tundra, have low primary productivity due to extreme temperatures and a shortage of available water.

Art Connections

Exercise:

   Problem:

   [link] Which of the following statements about biomes is false?

a. Chaparral is dominated by shrubs.
b. Savannas and temperate grasslands are dominated by grasses.
c. Boreal forests are dominated by deciduous trees.
d. Lichens are common in the arctic tundra.

Solution:

[link] C. Boreal forests are not dominated by deciduous trees.

Review Questions

Exercise:

Problem:

Which of the following biomes is characterized by abundant water resources?

a. deserts
b. boreal forests
c. savannas
d. tropical wet forests

Solution:

D

Exercise:

Problem:

Which of the following biomes is characterized by short growing seasons?

a. deserts
b. tropical wet forests
c. Arctic tundras

    d. savannas

Solution:

C

Free Response

Exercise:

Problem:

The extremely low precipitation of subtropical desert biomes might lead one to expect fire to be a major disturbance factor; however, fire is more common in the temperate grassland biome than in the subtropic desert biome. Why is this?

Solution:

Fire is less common in desert biomes than in temperate grasslands because deserts have low net primary productivity and, thus, very little plant biomass to fuel a fire.

Exercise:

Problem:

In what ways are the subtropical desert and the arctic tundra similar?

Solution:

Both the subtropical desert and the arctic tundra have a low supply of water. In the desert, this is due to extremely low precipitation, and in the arctic tundra, much of the water is unavailable to plants because it is frozen. Both the subtropical desert and the arctic tundra have low net primary productivity.

Glossary

canopy
> branches and foliage of trees that form a layer of overhead coverage in a forest

permafrost
> perennially frozen portion of the Arctic tundra soil

Aquatic Biomes
By the end of this section, you will be able to:

- Describe the effects of abiotic factors on the composition of plant and animal communities in aquatic biomes
- Compare and contrast the characteristics of the ocean zones
- Summarize the characteristics of standing water and flowing water freshwater biomes

Abiotic Factors Influencing Aquatic Biomes

Like terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. The aquatic medium—water— has different physical and chemical properties than air, however. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (like fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems. In freshwater systems, stratification due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

The ocean is categorized by several areas or zones ([link]). All of the ocean's open water is referred to as the **pelagic realm** (or zone). The **benthic realm** (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the **photic zone**, which is the portion of the ocean that light can penetrate (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the **aphotic zone**. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest

part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep. These realms and zones are relevant to freshwater lakes as well.

Note:
Art Connection
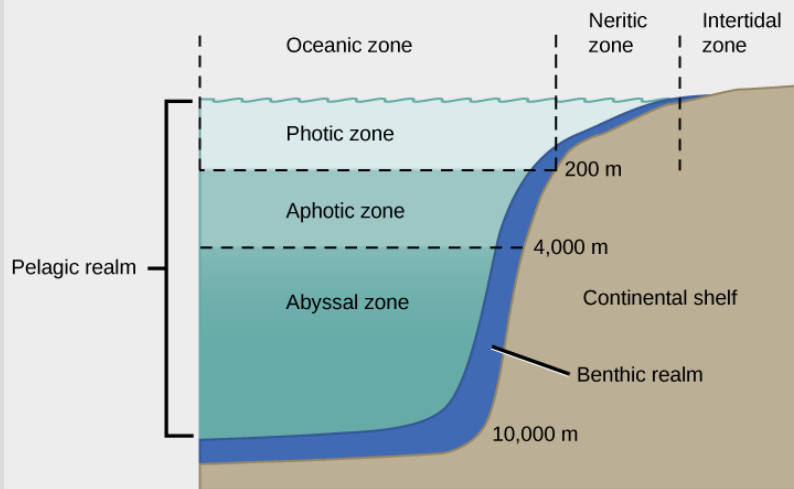
The ocean is divided into different zones based on water depth and distance from the shoreline.

In which of the following regions would you expect to find photosynthetic organisms?

a. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
b. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
c. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone
d. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

Marine Biomes

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome. Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

Ocean

The physical diversity of the ocean is a significant influence on plants, animals, and other organisms. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

The **intertidal zone**, which is the zone between high and low tide, is the oceanic region that is closest to land ([link]). Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy beach, but it can also be rocky or muddy. The intertidal zone is an extremely variable environment because of tides. Organisms are exposed to air and sunlight at low tide and are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. The shore of the intertidal zone is also repeatedly struck by waves, and the organisms found there are adapted to withstand damage from the pounding action of the waves ([link]). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from desiccation (drying out) and wave damage. Another consequence of the pounding waves is that few algae and plants establish themselves in the constantly moving rocks, sand, or mud.

Sea urchins, mussel shells, and starfish are often found in the intertidal zone, shown here in Kachemak Bay, Alaska. (credit: NOAA)

The **neritic zone** ([link]) extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the continental shelf. Since light can penetrate this depth, photosynthesis can occur in the neritic zone. The water here contains silt and is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating *Sargassum* (a type of free-floating marine seaweed) provide a habitat for some sea life found in the neritic zone. Zooplankton, protists, small fishes, and shrimp are found in the neritic zone and are the base of the food chain for most of the world's fisheries.

Beyond the neritic zone is the open ocean area known as the **oceanic zone** ([link]). Within the oceanic zone there is thermal stratification where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals such as whales and dolphins. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean where they remain; unlike freshwater lakes, the open ocean lacks a process for bringing the organic nutrients back up to the surface. The majority of organisms in the aphotic zone include sea cucumbers (phylum

Echinodermata) and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

Beneath the pelagic zone is the benthic realm, the deepwater region beyond the continental shelf ([link]). The bottom of the benthic realm is comprised of sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. This is a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exist.

The deepest part of the ocean is the **abyssal zone**, which is at depths of 4000 m or greater. The abyssal zone ([link]) is very cold and has very high pressure, high oxygen content, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants because of the lack of light. Hydrothermal vents are found primarily in the abyssal zone; chemosynthetic bacteria utilize the hydrogen sulfide and other minerals emitted from the vents. These chemosynthetic bacteria use the hydrogen sulfide as an energy source and serve as the base of the food chain found in the abyssal zone.

Coral Reefs

Coral reefs are ocean ridges formed by marine invertebrates living in warm shallow waters within the photic zone of the ocean. They are found within 30˚ north and south of the equator. The Great Barrier Reef is a well-known reef system located several miles off the northeastern coast of Australia. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms (members of phylum Cnidaria) are colonies of saltwater polyps that secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, forming the underwater reef ([link]). Corals found in shallower waters (at a depth of approximately 60 m or about 200 ft) have a mutualistic relationship with photosynthetic unicellular algae. The relationship provides corals with the majority of the nutrition and the energy they require. The waters in which

these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow. Some corals living in deeper and colder water do not have a mutualistic relationship with algae; these corals attain energy and nutrients using stinging cells on their tentacles to capture prey.

It is estimated that more than 4,000 fish species inhabit coral reefs. These fishes can feed on coral, the **cryptofauna** (invertebrates found within the calcium carbonate substrate of the coral reefs), or the seaweed and algae that are associated with the coral. In addition, some fish species inhabit the boundaries of a coral reef; these species include **predators**, herbivores, or **planktivores**. Predators are animal species that hunt and are carnivores or "flesh eaters." Herbivores eat plant material, and planktivores eat plankton.

Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria. (credit: Terry Hughes)

Note:
Evolution Connection
Global Decline of Coral Reefs
It takes a long time to build a coral reef. The animals that create coral reefs have evolved over millions of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic algal partners evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. As global warming due to fossil

fuel emissions raises ocean temperatures, coral reefs are suffering. The excessive warmth causes the reefs to expel their symbiotic, food-producing algae, resulting in a phenomenon known as bleaching. When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged. Rising levels of atmospheric carbon dioxide further threaten the corals in other ways; as CO_2 dissolves in ocean waters, it lowers the pH and increases ocean acidity. As acidity increases, it interferes with the calcification that normally occurs as coral animals build their calcium carbonate homes.

When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.

Human population growth has damaged corals in other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased, too, causing some of the once-clear tropical waters to become cloudy. At the same time, overfishing of popular fish species has allowed the predator species that eat corals to go unchecked. Although a rise in global temperatures of 1–2°C (a conservative scientific projection) in the coming decades may not seem large, it is very significant to this biome. When change occurs rapidly, species can become extinct before evolution leads to new adaptations. Many scientists believe that global warming, with its rapid (in terms of evolutionary time) and inexorable increases in temperature, is tipping the balance beyond the point at which many of the world's coral reefs can recover.

Estuaries: Where the Ocean Meets Fresh Water

Estuaries are biomes that occur where a source of fresh water, such as a river, meets the ocean. Therefore, both fresh water and salt water are found in the same vicinity; mixing results in a diluted (brackish) saltwater. Estuaries form protected areas where many of the young offspring of crustaceans, mollusks, and fish begin their lives. Salinity is a very important factor that influences the organisms and the adaptations of the organisms

found in estuaries. The salinity of estuaries varies and is based on the rate of flow of its freshwater sources. Once or twice a day, high tides bring salt water into the estuary. Low tides occurring at the same frequency reverse the current of salt water.

The short-term and rapid variation in salinity due to the mixing of fresh water and salt water is a difficult physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are halophytes: plants that can tolerate salty conditions. Halophytic plants are adapted to deal with the salinity resulting from saltwater on their roots or from sea spray. In some halophytes, filters in the roots remove the salt from the water that the plant absorbs. Other plants are able to pump oxygen into their roots. Animals, such as mussels and clams (phylum Mollusca), have developed behavioral adaptations that expend a lot of energy to function in this rapidly changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills) to anaerobic respiration (a process that does not require oxygen). When high tide returns to the estuary, the salinity and oxygen content of the water increases, and these animals open their shells, begin feeding, and return to aerobic respiration.

Freshwater Biomes

Freshwater biomes include lakes and ponds (standing water) as well as rivers and streams (flowing water). They also include wetlands, which will be discussed later. Humans rely on freshwater biomes to provide aquatic resources for drinking water, crop irrigation, sanitation, and industry. These various roles and human benefits are referred to as **ecosystem services**. Lakes and ponds are found in terrestrial landscapes and are, therefore, connected with abiotic and biotic factors influencing these terrestrial biomes.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. In the summer, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun and does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton (algae and cyanobacteria) are found here and carry out photosynthesis, providing the base of the food web of lakes and ponds. Zooplankton, such as rotifers and small crustaceans, consume these phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and phosphorus are important limiting nutrients in lakes and ponds. Because of this, they are determining factors in the amount of phytoplankton growth in lakes and ponds. When there is a large input of nitrogen and phosphorus (from sewage and runoff from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation of algae called an **algal bloom**. Algal blooms ([link]) can become so extensive that they reduce light penetration in water. As a result, the lake or pond becomes aphotic and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die, and resulting dead zones are found across the globe. Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and storm water runoff pose significant environmental challenges.

The uncontrolled growth of algae in this lake has resulted in an algal bloom. (credit: Jeremy Nettleton)

Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or headwater, to a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mississippi River in North America.

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as **source water**. The source water is usually cold, low in nutrients, and clear. The **channel** (the width of the river or stream) is narrower than at any other place along the length of the river or stream. Because of this, the current is often faster here than at any other point of the river or stream.

The fast-moving water results in minimal silt accumulation at the bottom of the river or stream; therefore, the water is clear. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton. An additional input of energy can

come from leaves or other organic material that falls into the river or stream from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, leeches (phylum Annelida) have elongated bodies and suckers on both ends. These suckers attach to the substrate, keeping the leech anchored in place. Freshwater trout species (phylum Chordata) are an important predator in these fast-moving rivers and streams.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer. Worms (phylum Annelida) and insects (phylum Arthropoda) can be found burrowing into the mud. The higher order predator vertebrates (phylum Chordata) include waterfowl, frogs, and fishes. These predators must find food in these slow moving, sometimes murky, waters and, unlike the trout in the waters at the source, these vertebrates may not be able to use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes because wetlands are shallow bodies of water whereas lakes vary in depth. **Emergent vegetation** consists of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes ([link]). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.

Located in southern Florida, Everglades National Park is vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. (credit: NPS)

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation. Percolation is the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen depleted because the oxygen that is used during the decomposition of organic matter is not replaced. As the oxygen in the water is depleted, decomposition slows. This leads to organic acids and other acids building up and lowering the pH of the water. At a lower pH, nitrogen becomes unavailable to plants. This creates a challenge for plants because nitrogen is an important limiting resource. Some types of bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects and extract the nitrogen from their bodies. Bogs have low net primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

Section Summary

Aquatic ecosystems include both saltwater and freshwater biomes. The abiotic factors important for the structuring of aquatic ecosystems can be different than those seen in terrestrial systems. Sunlight is a driving force behind the structure of forests and also is an important factor in bodies of water, especially those that are very deep, because of the role of photosynthesis in sustaining certain organisms. Density and temperature shape the structure of aquatic systems. Oceans may be thought of as consisting of different zones based on water depth and distance from the shoreline and light penetrance. Different kinds of organisms are adapted to the conditions found in each zone. Coral reefs are unique marine ecosystems that are home to a wide variety of species. Estuaries are found where rivers meet the ocean; their shallow waters provide nourishment and shelter for young crustaceans, mollusks, fishes, and many other species. Freshwater biomes include lakes, ponds, rivers, streams, and wetlands. Bogs are an interesting type of wetland characterized by standing water, lower pH, and a lack of nitrogen.

Art Connections

Exercise:

Problem:

[link] In which of the following regions would you expect to find photosynthetic organisms?

- a. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
- b. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
- c. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone
- d. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

Solution:

[link] C. Photosynthetic organisms would be found in the photic, abyssal, neritic, and oceanic zones.

Review Questions

Exercise:

Problem:

Where would you expect to find the most photosynthesis in an ocean biome?

  a. aphotic zone
  b. abyssal zone
  c. benthic realm
  d. intertidal zone

Solution:

D

Exercise:

Problem: A key feature of estuaries is:

  a. low light conditions and high productivity
  b. salt water and fresh water
  c. frequent algal blooms
  d. little or no vegetation

Solution:

B

Free Response

Exercise:

Problem:

Scientists have discovered the bodies of humans and other living things buried in bogs for hundreds of years, but not yet decomposed. Suggest a possible biological explanation for why such bodies are so well-preserved.

Solution:

Bogs are low in oxygen and high in organic acids. The low oxygen content and the low pH both slow the rate of decomposition.

Exercise:

Problem:

Describe the conditions and challenges facing organisms living in the intertidal zone.

Solution:

Organisms living in the intertidal zone must tolerate periodic exposure to air and sunlight and must be able to be periodically dry. They also must be able to endure the pounding waves; for this reason, some shoreline organisms have hard exoskeletons that provide protection while also reducing the likelihood of drying out.

Glossary

abyssal zone
    deepest part of the ocean at depths of 4000 m or greater

algal bloom
    rapid increase of algae in an aquatic system

aphotic zone
    part of the ocean where no light penetrates

benthic realm
    (also, benthic zone) part of the ocean that extends along the ocean
    bottom from the shoreline to the deepest parts of the ocean floor

channel
    width of a river or stream from one bank to the other bank

coral reef
    ocean ridges formed by marine invertebrates living in warm, shallow
    waters within the photic zone

cryptofauna
    invertebrates found within the calcium carbonate substrate of coral
    reefs

ecosystem services
    human benefits and services provided by natural ecosystems

emergent vegetation
    wetland plants that are rooted in the soil but have portions of leaves,
    stems, and flowers extending above the water's surface

estuary
    biomes where a source of fresh water, such as a river, meets the ocean

intertidal zone
    part of the ocean that is closest to land; parts extend above the water at
    low tide

neritic zone
    part of the ocean that extends from low tide to the edge of the
    continental shelf

oceanic zone
    part of the ocean that begins offshore where the water measures 200 m
    deep or deeper

pelagic realm

(also, pelagic zone) open ocean waters that are not close to the bottom or near the shore

photic zone
portion of the ocean that light can penetrate

planktivore
animal species that eats plankton

predator
animal species that hunt and are carnivores or "flesh eaters"

Sargassum
type of free-floating marine seaweed

source water
point of origin of a river or stream

Introduction
class="introduction"

Asian carp jump out of the water in response to electrofishing. The Asian carp in the inset photograph were harvested from the Little Calumet River in Illinois in May, 2010, using rotenone, a toxin often used as an insecticide, in an effort to learn more about the population of the species. (credit main image: modification of work by USGS; credit inset: modification

of work by
Lt. David
French,
USCG)

Imagine sailing down a river in a small motorboat on a weekend afternoon; the water is smooth and you are enjoying the warm sunshine and cool breeze when suddenly you are hit in the head by a 20-pound silver carp. This is a risk now on many rivers and canal systems in Illinois and Missouri because of the presence of Asian carp.

This fish—actually a group of species including the silver, black, grass, and big head carp—has been farmed and eaten in China for over 1000 years. It is one of the most important aquaculture food resources worldwide. In the United States, however, Asian carp is considered a dangerous invasive species that disrupts community structure and composition to the point of threatening native species.

Population Demography
By the end of this section, you will be able to:

- Describe how ecologists measure population size and density
- Describe three different patterns of population distribution
- Use life tables to calculate mortality rates
- Describe the three types of survivorship curves and relate them to specific populations

Populations are dynamic entities. Populations consist all of the species living within a specific area, and populations fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. The statistical study of population dynamics, **demography**, uses a series of mathematical tools to investigate how populations respond to changes in their biotic and abiotic environments. Many of these tools were originally designed to study human populations. For example, **life tables**, which detail the life expectancy of individuals within a population, were initially developed by life insurance companies to set insurance rates. In fact, while the term "demographics" is commonly used when discussing humans, all living populations can be studied using this approach.

Population Size and Density

The study of any population usually begins by determining how many individuals of a particular species exist, and how closely associated they are with each other. Within a particular habitat, a population can be characterized by its **population size (N)**, the total number of individuals, and its **population density**, the number of individuals within a specific area or volume. Population size and density are the two main characteristics used to describe and understand populations. For example, populations with more individuals may be more stable than smaller populations based on their genetic variability, and thus their potential to adapt to the environment. Alternatively, a member of a population with low population density (more spread out in the habitat), might have more difficulty finding a mate to

reproduce compared to a population of higher density. As is shown in [link], smaller organisms tend to be more densely distributed than larger organisms.

Note:
Art Connection

Relationship between Population and Body Mass in Australian Mammals
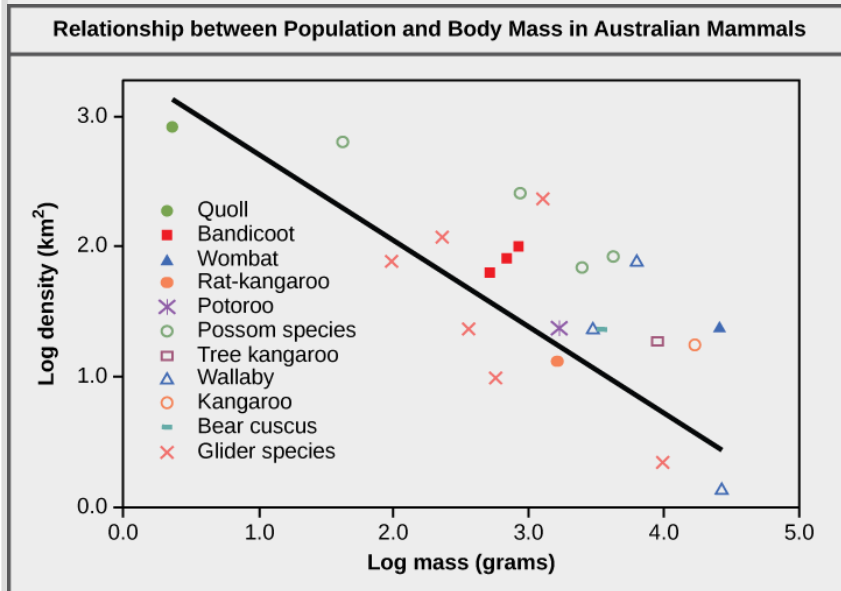
Australian mammals show a typical inverse relationship between population density and body size.

As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

Population Research Methods

The most accurate way to determine population size is to simply count all of the individuals within the habitat. However, this method is often not logistically or economically feasible, especially when studying large habitats. Thus, scientists usually study populations by sampling a representative portion of each habitat and using this data to make inferences

about the habitat as a whole. A variety of methods can be used to sample populations to determine their size and density. For immobile organisms such as plants, or for very small and slow-moving organisms, a **quadrat** may be used ([link]). A quadrat is a way of marking off square areas within a habitat, either by staking out an area with sticks and string, or by the use of a wood, plastic, or metal square placed on the ground. After setting the quadrats, researchers then count the number of individuals that lie within their boundaries. Multiple quadrat samples are performed throughout the habitat at several random locations. All of this data can then be used to estimate the population size and population density within the entire habitat. The number and size of quadrat samples depends on the type of organisms under study and other factors, including the density of the organism. For example, if sampling daffodils, a 1 m^2 quadrat might be used whereas with giant redwoods, which are larger and live much further apart from each other, a larger quadrat of 100 m^2 might be employed. This ensures that enough individuals of the species are counted to get an accurate sample that correlates with the habitat, including areas not sampled.
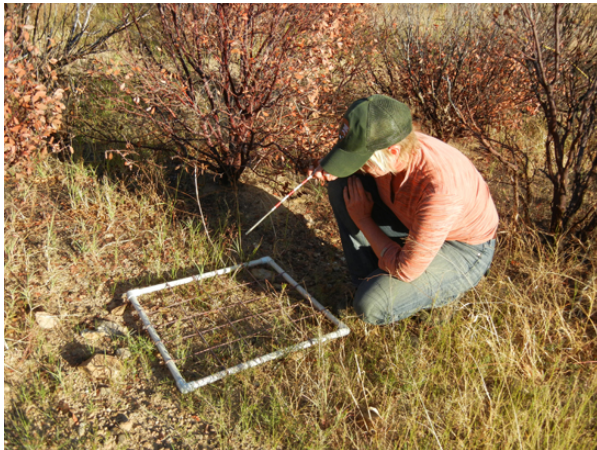
A scientist uses a quadrat to measure population size and density. (credit: NPS Sonoran Desert Network)

For mobile organisms, such as mammals, birds, or fish, a technique called **mark and recapture** is often used. This method involves marking a sample of captured animals in some way (such as tags, bands, paint, or other body markings), and then releasing them back into the environment to allow them to mix with the rest of the population; later, a new sample is collected, including some individuals that are marked (recaptures) and some individuals that are unmarked ([link]).

(a)   (b)   (c)

Mark and recapture is used to measure the population size of mobile animals such as (a) bighorn sheep, (b) the California condor, and (c) salmon. (credit a: modification of work by Neal Herbert, NPS; credit b: modification of work by Pacific Southwest Region USFWS; credit c: modification of work by Ingrid Taylar)

Using the ratio of marked and unmarked individuals, scientists determine how many individuals are in the sample. From this, calculations are used to estimate the total population size. This method assumes that the larger the population, the lower the percentage of tagged organisms that will be recaptured since they will have mixed with more untagged individuals. For example, if 80 deer are captured, tagged, and released into the forest, and later 100 deer are captured and 20 of them are already marked, we can determine the population size (N) using the following equation:

Equation:

$$\frac{(\text{number marked first catch x total number of second catch})}{\text{number marked second catch}} = N$$

Using our example, the population size would be estimated at 400.
Equation:

$$\frac{(80 \text{ x } 100)}{20} = 400$$

Therefore, there are an estimated 400 total individuals in the original population.

There are some limitations to the mark and recapture method. Some animals from the first catch may learn to avoid capture in the second round, thus inflating population estimates. Alternatively, animals may preferentially be retrapped (especially if a food reward is offered), resulting in an underestimate of population size. Also, some species may be harmed by the marking technique, reducing their survival. A variety of other techniques have been developed, including the electronic tracking of animals tagged with radio transmitters and the use of data from commercial fishing and trapping operations to estimate the size and health of populations and communities.

Species Distribution

In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals. **Species dispersion patterns** (or distribution patterns) show the spatial relationship between members of a population within a habitat at a particular point in time. In other words, they show whether members of the species live close together or far apart, and what patterns are evident when they are spaced apart.

Individuals in a population can be more or less equally spaced apart, dispersed randomly with no predictable pattern, or clustered in groups. These are known as uniform, random, and clumped dispersion patterns,

respectively ([link]). Uniform dispersion is observed in plants that secrete substances inhibiting the growth of nearby individuals (such as the release of toxic chemicals by the sage plant *Salvia leucophylla,* a phenomenon called allelopathy) and in animals like the penguin that maintain a defined territory. An example of random dispersion occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in a favorable environment. A clumped dispersion may be seen in plants that drop their seeds straight to the ground, such as oak trees, or animals that live in groups (schools of fish or herds of elephants). Clumped dispersions may also be a function of habitat heterogeneity. Thus, the dispersion of the individuals within a population provides more information about how they interact with each other than does a simple density measurement. Just as lower density species might have more difficulty finding a mate, solitary species with a random distribution might have a similar difficulty when compared to social species clumped together in groups.
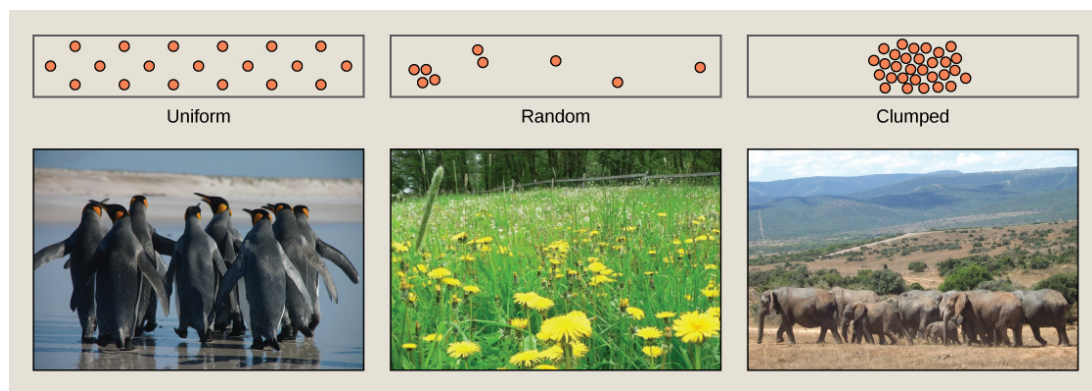
Species may have uniform, random, or clumped distribution. Territorial birds such as penguins tend to have uniform distribution. Plants such as dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as elephants that travel in groups exhibit clumped distribution. (credit a: modification of work by Ben Tubby; credit b: modification of work by Rosendahl; credit c: modification of work by Rebecca Wood)

Demography

While population size and density describe a population at one particular point in time, scientists must use demography to study the dynamics of a population. Demography is the statistical study of population changes over time: birth rates, death rates, and life expectancies. Each of these measures, especially birth rates, may be affected by the population characteristics described above. For example, a large population size results in a higher birth rate because more potentially reproductive individuals are present. In contrast, a large population size can also result in a higher death rate because of competition, disease, and the accumulation of waste. Similarly, a higher population density or a clumped dispersion pattern results in more potential reproductive encounters between individuals, which can increase birth rate. Lastly, a female-biased sex ratio (the ratio of males to females) or age structure (the proportion of population members at specific age ranges) composed of many individuals of reproductive age can increase birth rates.

In addition, the demographic characteristics of a population can influence how the population grows or declines over time. If birth and death rates are equal, the population remains stable. However, the population size will increase if birth rates exceed death rates; the population will decrease if birth rates are less than death rates. Life expectancy is another important factor; the length of time individuals remain in the population impacts local resources, reproduction, and the overall health of the population. These demographic characteristics are often displayed in the form of a life table.

Life Tables

Life tables provide important information about the life history of an organism. Life tables divide the population into age groups and often sexes, and show how long a member of that group is likely to live. They are modeled after actuarial tables used by the insurance industry for estimating human life expectancy. Life tables may include the probability of individuals dying before their next birthday (i.e., their **mortality rate**), the

percentage of surviving individuals dying at a particular age interval, and their life expectancy at each interval. An example of a life table is shown in [link] from a study of Dall mountain sheep, a species native to northwestern North America. Notice that the population is divided into age intervals (column A). The mortality rate (per 1000), shown in column D, is based on the number of individuals dying during the age interval (column B) divided by the number of individuals surviving at the beginning of the interval (Column C), multiplied by 1000.

Equation:

$$\text{mortality rate} = \frac{\text{number of individuals dying}}{\text{number of individuals surviving}} \text{ x } 1000$$

For example, between ages three and four, 12 individuals die out of the 776 that were remaining from the original 1000 sheep. This number is then multiplied by 1000 to get the mortality rate per thousand.

Equation:

$$\text{mortality rate} = \frac{12}{776} \text{ x } 1000 \approx 15.5$$

As can be seen from the mortality rate data (column D), a high death rate occurred when the sheep were between 6 and 12 months old, and then increased even more from 8 to 12 years old, after which there were few survivors. The data indicate that if a sheep in this population were to survive to age one, it could be expected to live another 7.7 years on average, as shown by the life expectancy numbers in column E.

Life Table of Dall Mountain Sheep[footnote]
Data Adapted from Edward S. Deevey, Jr., "Life Tables for Natural Populations of Animals," *The Quarterly Review of Biology* **22, no. 4 (December 1947): 283-314.**

Age interval (years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 alive at beginning of age interval	Life expectancy or mean lifetime remaining to those attaining age interval
0-0.5	54	1000	54.0	7.06
0.5-1	145	946	153.3	--
1-2	12	801	15.0	7.7
2-3	13	789	16.5	6.8
3-4	12	776	15.5	5.9
4-5	30	764	39.3	5.0
5-6	46	734	62.7	4.2
6-7	48	688	69.8	3.4
7-8	69	640	107.8	2.6
8-9	132	571	231.2	1.9
9-10	187	439	426.0	1.3

10-11	156	252	619.0	0.9
11-12	90	96	937.5	0.6
12-13	3	6	500.0	1.2
13-14	3	3	1000	0.7

This life table of *Ovis dalli* shows the number of deaths, number of survivors, mortality rate, and life expectancy at each age interval for the Dall mountain sheep.

Survivorship Curves

Another tool used by population ecologists is a **survivorship curve**, which is a graph of the number of individuals surviving at each age interval plotted versus time (usually with data compiled from a life table). These curves allow us to compare the life histories of different populations ([link]). Humans and most primates exhibit a Type I survivorship curve because a high percentage of offspring survive their early and middle years—death occurs predominantly in older individuals. These types of species usually have small numbers of offspring at one time, and they give a high amount of parental care to them to ensure their survival. Birds are an example of an intermediate or Type II survivorship curve because birds die more or less equally at each age interval. These organisms also may have relatively few offspring and provide significant parental care. Trees, marine invertebrates, and most fishes exhibit a Type III survivorship curve because very few of these organisms survive their younger years; however, those that make it to an old age are more likely to survive for a relatively long period of time. Organisms in this category usually have a very large number of offspring, but once they are born, little parental care is provided. Thus these offspring are "on their own" and vulnerable to predation, but their sheer numbers assure the survival of enough individuals to perpetuate the species.

Survivorship Curve

Type I (humans)

Type II (birds)

Type III (trees)

Number of individuals surviving (log scale)

Percentage of maximum life expectancy

0   50   100
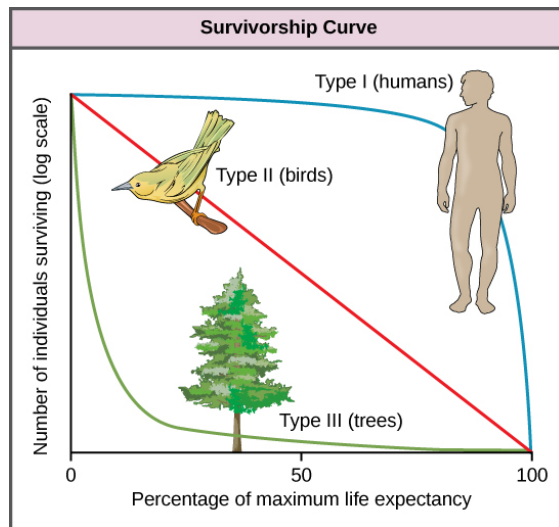
Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

Section Summary

Populations are individuals of a species that live in a particular habitat. Ecologists measure characteristics of populations: size, density, dispersion pattern, age structure, and sex ratio. Life tables are useful to calculate life

expectancies of individual population members. Survivorship curves show the number of individuals surviving at each age interval plotted versus time.

Art Connections

Exercise:

Problem:

[link] As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

Solution:

[link] Smaller animals require less food and other resources, so the environment can support more of them.

Review Questions

Exercise:

Problem:

Which of the following methods will tell an ecologist about both the size and density of a population?

  a. mark and recapture
  b. mark and release
  c. quadrat
  d. life table

Solution:

C

Exercise:

Problem:

Which of the following is best at showing the life expectancy of an individual within a population?

    a. quadrat
    b. mark and recapture
    c. survivorship curve
    d. life table

Solution:

D

Exercise:

Problem: Humans have which type of survivorship curve?

    a. Type I
    b. Type II
    c. Type III
    d. Type IV

Solution:

A

Free Response

Exercise:

Problem:

Describe how a researcher would determine the size of a penguin population in Antarctica using the mark and release method.

Solution:

The researcher would mark a certain number of penguins with a tag, release them back into the population, and, at a later time, recapture penguins to see what percentage of the recaptured penguins was tagged. This percentage would allow an estimation of the size of the penguin population.

Glossary

demography
      statistical study of changes in populations over time

life table
      table showing the life expectancy of a population member based on its age

mark and recapture
      technique used to determine population size in mobile organisms

mortality rate
      proportion of population surviving to the beginning of an age interval that die during the age interval

population density
      number of population members divided by the area or volume being measured

population size (*N*)
      number of population members in a habitat at the same time

quadrat
      square made of various materials used to determine population size and density in slow moving or stationary organisms

species dispersion pattern

(also, species distribution pattern) spatial location of individuals of a given species within a habitat at a particular point in time

survivorship curve
graph of the number of surviving population members versus the relative age of the member

Environmental Limits to Population Growth
By the end of this section, you will be able to:

- Explain the characteristics of and differences between exponential and logistic growth patterns
- Give examples of exponential and logistic growth in natural populations
- Describe how natural selection and environmental adaptation led to the evolution of particular life history patterns

Although life histories describe the way many characteristics of a population (such as their age structure) change over time in a general way, population ecologists make use of a variety of methods to model population dynamics mathematically. These more precise models can then be used to accurately describe changes occurring in a population and better predict future changes. Certain models that have been accepted for decades are now being modified or even abandoned due to their lack of predictive ability, and scholars strive to create effective new models.

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, and then population growth decreases as resources become depleted. This accelerating pattern of increasing population size is called **exponential growth**.

The best example of exponential growth is seen in bacteria. Bacteria are prokaryotes that reproduce by prokaryotic fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour, there is one round of division and each organism divides, resulting in 2000 organisms—an increase of 1000. In another hour, each of the 2000 organisms will double, producing 4000, an increase of 2000 organisms. After the third hour, there should be 8000 bacteria in the flask, an increase of 4000 organisms. The important concept of exponential

growth is that the **population growth rate**—the number of organisms added in each reproductive generation—is accelerating; that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the population would have increased from 1000 to more than 16 billion. When the population size, *N*, is plotted over time, a **J-shaped growth curve** is produced ([link]).

The bacteria example is not representative of the real world where resources are limited. Furthermore, some bacteria will die during the experiment and thus not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the **death rate (*D*)** (number organisms that die during a particular time interval) is subtracted from the **birth rate (*B*)** (number organisms that are born during that interval). This is shown in the following formula:
Equation:

$$\frac{\Delta N \text{ (change in number)}}{\Delta T \text{ (change in time)}} = B \text{ (birth rate) - } D \text{ (death rate)}$$

The birth rate is usually expressed on a per capita (for each individual) basis. Thus, *B* (birth rate) = *bN* (the per capita birth rate "*b*" multiplied by the number of individuals "*N*") and *D* (death rate) =*dN* (the per capita death rate "*d*" multiplied by the number of individuals "*N*"). Additionally, ecologists are interested in the population at a particular point in time, an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the "instantaneous" growth rate, replacing the *change* in number and time with an instant-specific measurement of number and time.
Equation:

$$\frac{dN}{dT} = bN - dN = (b - d)N$$

Notice that the "*d*" associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called "*d*." The difference between birth and death rates is further simplified by

substituting the term "*r*" (intrinsic rate of increase) for the relationship between birth and death rates:

Equation:

$$\frac{dN}{dT} = rN$$

The value "*r*" can be positive, meaning the population is increasing in size; or negative, meaning the population is decreasing in size; or zero, where the population's size is unchanging, a condition known as **zero population growth**. A further refinement of the formula recognizes that different species have inherent differences in their intrinsic rate of increase (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its **biotic potential, or r_{max}**, thus changing the equation to:

Equation:

$$\frac{dN}{dT} = r_{\max}N$$

Exponential Growth	Logistic Growth
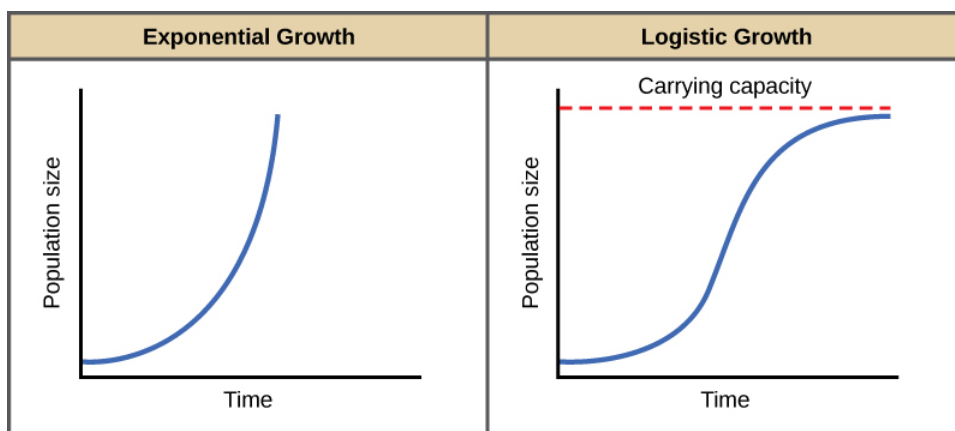
When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit

logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

Logistic Growth

Exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the "struggle for existence," which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the **logistic growth** model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off ([link]). This population size, which represents the maximum population size that a particular environment can support, is called the **carrying capacity, or K**.

The formula we use to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression "$K - N$" is indicative of how many individuals may be added to a population at a given stage, and "$K - N$" divided by "K" is the fraction of the carrying capacity

available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:
Equation:

$$\frac{dN}{dT} = r_{\max}\frac{dN}{dT} = r_{\max}N\frac{(K \; - \; N)}{K}$$

Notice that when N is very small, $(K\text{-}N)/K$ becomes close to K/K or 1, and the right side of the equation reduces to $r_{max}N$, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when N is large, $(K\text{-}N)/K$ come close to zero, which means that population growth will be slowed greatly or even stopped. Thus, population growth is greatly slowed in large populations by the carrying capacity K. This model also allows for the population of a negative population growth, or a population decline. This occurs when the number of individuals in the population exceeds the carrying capacity (because the value of (K-N)/K is negative).

A graph of this equation yields an **S-shaped curve** ([link]), and it is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition** (intra- = "within"; -specific = "species"). Intraspecific competition for resources may not affect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment's carrying capacity.

Examples of Logistic Growth

Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube ([link]**a**). Its growth levels off as the population depletes the nutrients that are necessary for its growth. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals ([link]**b**). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

Note:
Art Connection
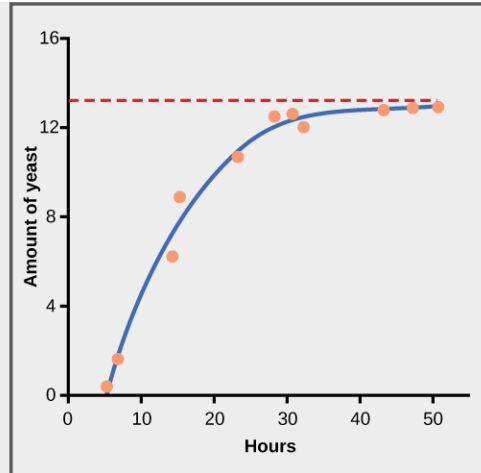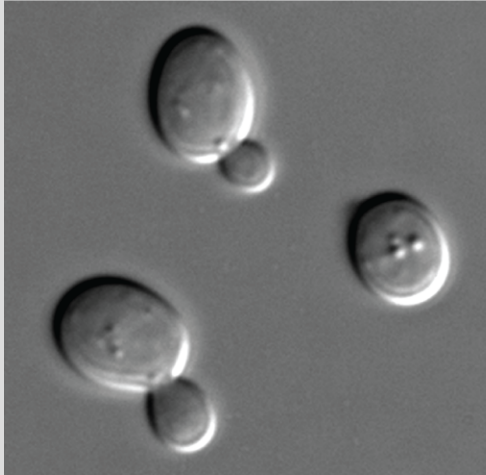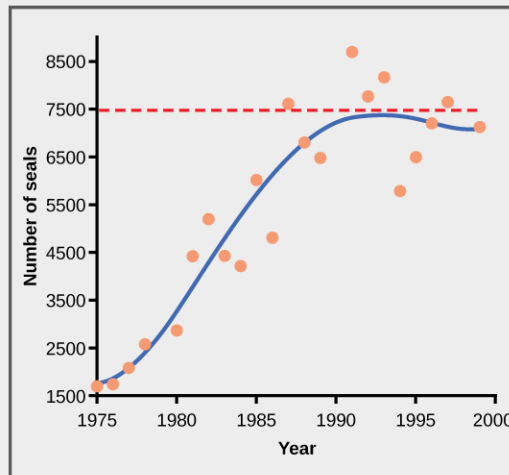
(a) Yeast grown in ideal conditions in a test tube show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.

If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

a. The carrying capacity of seals would decrease, as would the seal population.
b. The carrying capacity of seals would decrease, but the seal population would remain the same.

c. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
d. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Section Summary

Populations with unlimited resources grow exponentially, with an accelerating growth rate. When resources become limiting, populations follow a logistic growth curve. The population of a species will level off at the carrying capacity of its environment.

Art Connections

Exercise:

  Problem:

  [link]**b** If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

   a. The carrying capacity of seals would decrease, as would the seal population.
   b. The carrying capacity of seals would decrease, but the seal population would remain the same.
   c. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
   d. The carrying capacity of seals would remain the same, but the population of seals would decrease.

  Solution:

[link]**b** A

Review Questions

Exercise:

Problem:

Species with limited resources usually exhibit a(n) _____ growth curve.

  a. logistic
  b. logical
  c. experimental
  d. exponential

Solution:

A

Exercise:

Problem:

The maximum rate of increased characteristic of a species is called its _____.

  a. limit
  b. carrying capacity
  c. biotic potential
  d. exponential growth pattern

Solution:

C

Exercise:

Problem:

The population size of a species capable of being supported by the environment is called its _____.

   a. limit
   b. carrying capacity
   c. biotic potential
   d. logistic growth pattern

Solution:

B

Free Response

Exercise:

Problem:

Describe the rate of population growth that would be expected at various parts of the S-shaped curve of logistic growth.

Solution:

In the first part of the curve, when few individuals of the species are present and resources are plentiful, growth is exponential, similar to a J-shaped curve. Later, growth slows due to the species using up resources. Finally, the population levels off at the carrying capacity of the environment, and it is relatively stable over time.

Glossary

biotic potential (r_{max})
    maximal potential growth rate of a species

birth rate (*B*)
    number of births within a population at a specific point in time

carrying capacity (*K*)
    number of individuals of a species that can be supported by the limited resources of a habitat

death rate (*D*)
    number of deaths within a population at a specific point in time

exponential growth
    accelerating growth pattern seen in species under conditions where resources are not limiting

intraspecific competition
    competition between members of the same species

J-shaped growth curve
    shape of an exponential growth curve

logistic growth
    leveling off of exponential growth due to limiting resources

population growth rate
    number of organisms added in each reproductive generation

S-shaped growth curve
    shape of a logistic growth curve

zero population growth
    steady population size where birth rates and death rates are equal

Population Dynamics and Regulation
By the end of this section, you will be able to:

- Give examples of how the carrying capacity of a habitat may change
- Compare and contrast density-dependent growth regulation and density-independent growth regulation, giving examples
- Give examples of exponential and logistic growth in wild animal populations
- Describe how natural selection and environmental adaptation leads to the evolution of particular life-history patterns

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. The carrying capacity varies annually: for example, some summers are hot and dry whereas others are cold and wet. In many areas, the carrying capacity during the winter is much lower than it is during the summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They engage in **interspecific competition**: that is, they share the environment with other species, competing with them for the same resources. These factors are also important to understanding how a specific population will grow.

Nature regulates population growth in a variety of ways. These are grouped into **density-dependent** factors, in which the density of the population at a given time affects growth rate and mortality, and **density-independent** factors, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Density-dependent Regulation

Most density-dependent factors are biological in nature (biotic), and include predation, inter- and intraspecific competition, accumulation of waste, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown in [link] with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals.[footnote] Denser populations of the parasite exhibited lower fecundity: they contained fewer eggs. One possible explanation for this is that females would be smaller in more dense populations (due to limited resources) and that smaller females would have fewer eggs. This hypothesis was tested and disproved in a 2009 study which showed that female weight had no influence.[footnote] The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

N.A. Croll et al., "The Population Biology and Control of *Ascaris lumbricoides* in a Rural Community in Iran." *Transactions of the Royal Society of Tropical Medicine and Hygiene* 76, no. 2 (1982): 187-197, doi:10.1016/0035-9203(82)90272-3.

Martin Walker et al., "Density-Dependent Effects on the Weight of Female *Ascaris lumbricoides* Infections of Humans and its Impact on Patterns of Egg Production." *Parasites & Vectors* 2, no. 11 (February 2009), doi:10.1186/1756-3305-2-11.

Fecundity as a Function of Population
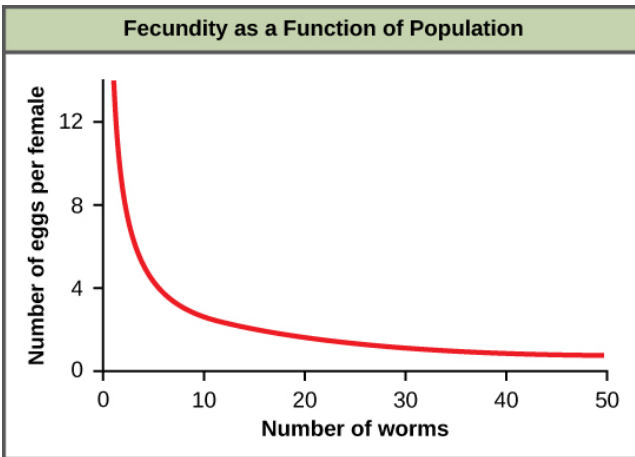
In this population of roundworms, fecundity (number of eggs) decreases with population density. [footnote]

N.A. Croll et al., "The Population Biology and Control of *Ascaris lumbricoides* in a Rural Community in Iran." *Transactions of the Royal Society of Tropical Medicine and Hygiene* 76, no. 2 (1982): 187-197, doi:10.1016/0035-9203(82)90272-3.

Density-independent Regulation and Interaction with Density-dependent Factors

Many factors, typically physical or chemical in nature (abiotic), influence the mortality of a population regardless of its density, including weather, natural disasters, and pollution. An individual deer may be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

Note:
Evolution Connection
Why Did the Woolly Mammoth Go Extinct?

The three photos include: (a) 1916 mural of a mammoth herd from the American Museum of Natural History, (b) the only stuffed mammoth in the world, from the Museum of Zoology located in St. Petersburg, Russia, and (c) a one-month-old baby mammoth, named Lyuba, discovered in Siberia in 2007. (credit a: modification of work by Charles R. Knight; credit b: modification of work by "Tanapon"/Flickr; credit c: modification of work by Matt Howry)

It's easy to get lost in the discussion of dinosaurs and theories about why they went extinct 65 million years ago. Was it due to a meteor slamming into Earth near the coast of modern-day Mexico, or was it from some long-term weather cycle that is not yet understood? One hypothesis that will never be proposed is that humans had something to do with it. Mammals were small, insignificant creatures of the forest 65 million years ago, and no humans existed.

Woolly mammoths, however, began to go extinct about 10,000 years ago, when they shared the Earth with humans who were no different

anatomically than humans today ([link]). Mammoths survived in isolated island populations as recently as 1700 BC. We know a lot about these animals from carcasses found frozen in the ice of Siberia and other regions of the north. Scientists have sequenced at least 50 percent of its genome and believe mammoths are between 98 and 99 percent identical to modern elephants.

It is commonly thought that climate change and human hunting led to their extinction. A 2008 study estimated that climate change reduced the mammoth's range from 3,000,000 square miles 42,000 years ago to 310,000 square miles 6,000 years ago.[footnote] It is also well documented that humans hunted these animals. A 2012 study showed that no single factor was exclusively responsible for the extinction of these magnificent creatures.[footnote] In addition to human hunting, climate change, and reduction of habitat, these scientists demonstrated another important factor in the mammoth's extinction was the migration of humans across the Bering Strait to North America during the last ice age 20,000 years ago. David Nogués-Bravo et al., "Climate Change, Humans, and the Extinction of the Woolly Mammoth." *PLoS Biol* 6 (April 2008): e79, doi:10.1371/journal.pbio.0060079. G.M. MacDonald et al., "Pattern of Extinction of the Woolly Mammoth in Beringia." *Nature Communications* 3, no. 893 (June 2012), doi:10.1038/ncomms1881. The maintenance of stable populations was and is very complex, with many interacting factors determining the outcome. It is important to remember that humans are also part of nature. Once we contributed to a species' decline using primitive hunting technology only.

Life Histories of *K*-selected and *r*-selected Species

While reproductive strategies play a key role in life histories, they do not account for important factors like limited resources and competition. The regulation of population growth by these factors can be used to introduce a classical concept in population biology, that of *K*-selected versus *r*-selected species.

Early Theories about Life History: *K*-selected and *r*-selected Species

By the second half of the twentieth century, the concept of K- and r-selected species was used extensively and successfully to study populations. The concept relates not only reproductive strategies, but also to a species' habitat and behavior, especially in the way that they obtain resources and care for their young. It includes length of life and survivorship factors as well. For this analysis, population biologists have grouped species into the two large categories—*K*-selected and *r*-selected—although they are really two ends of a continuum.

K-selected species are species selected by stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity (hence the term *K*-selected) where intraspecific competition is high. These species have few, large offspring, a long gestation period, and often give long-term care to their offspring (Table B45_04_01). While larger in size when born, the offspring are relatively helpless and immature at birth. By the time they reach adulthood, they must develop skills to compete for natural resources. In plants, scientists think of parental care more broadly: how long fruit takes to develop or how long it remains on the plant are determining factors in the time to the next reproductive event. Examples of *K*-selected species are primates including humans), elephants, and plants such as oak trees ([link]**a**).

Oak trees grow very slowly and take, on average, 20 years to produce their first seeds, known as acorns. As many as 50,000 acorns can be produced by an individual tree, but the germination rate is low as many of these rot or are eaten by animals such as squirrels. In some years, oaks may produce an exceptionally large number of acorns, and these years may be on a two- or three-year cycle depending on the species of oak (*r*-selection).

As oak trees grow to a large size and for many years before they begin to produce acorns, they devote a large percentage of their energy budget to growth and maintenance. The tree's height and size allow it to dominate other plants in the competition for sunlight, the oak's primary energy resource. Furthermore, when it does reproduce, the oak produces large, energy-rich seeds that use their energy reserve to become quickly established (*K*-selection).

In contrast, **r-selected species** have a large number of small offspring (hence their *r* designation ([link]). This strategy is often employed in unpredictable or changing environments. Animals that are *r*-selected do not give long-term parental care and the offspring are relatively mature and self-sufficient at birth. Examples of *r*-selected species are marine invertebrates, such as jellyfish, and plants, such as the dandelion ([link]**b**). Dandelions have small seeds that are wind dispersed long distances. Many seeds are produced simultaneously to ensure that at least some of them reach a hospitable environment. Seeds that land in inhospitable environments have little chance for survival since their seeds are low in energy content. Note that survival is not necessarily a function of energy stored in the seed itself.

Characteristics of *K*-selected and *r*-selected species	
Characteristics of *K*-selected species	**Characteristics of *r*-selected species**
Mature late	Mature early
Greater longevity	Lower longevity
Increased parental care	Decreased parental care
Increased competition	Decreased competition
Fewer offspring	More offspring
Larger offspring	Smaller offspring

(a) K-selected species

(b) r-selected species

(a) Elephants are considered K-selected species as they live long, mature late, and provide long-term parental care to few offspring. Oak trees produce many offspring that do not receive parental care, but are considered K-selected species based on longevity and late maturation. (b) Dandelions and jellyfish are both considered r-selected species as they mature early, have short lifespans, and produce many offspring that receive no parental care.

Modern Theories of Life History

The *r*- and *K*-selection theory, although accepted for decades and used for much groundbreaking research, has now been reconsidered, and many population biologists have abandoned or modified it. Over the years, several studies attempted to confirm the theory, but these attempts have largely failed. Many species were identified that did not follow the theory's

predictions. Furthermore, the theory ignored the age-specific mortality of the populations which scientists now know is very important. New **demographic-based models** of life history evolution have been developed which incorporate many ecological concepts included in *r*- and *K*-selection theory as well as population age structure and mortality factors.

Section Summary

Populations are regulated by a variety of density-dependent and density-independent factors. Species are divided into two categories based on a variety of features of their life history patterns: *r*-selected species, which have large numbers of offspring, and *K*-selected species, which have few offspring. The *r*- and *K*-selection theory has fallen out of use; however, many of its key features are still used in newer, demographically-based models of population dynamics.

Review Questions

Exercise:

   Problem: Species that have many offspring at one time are usually:

      a. *r*-selected
      b. *K*-selected
      c. both *r*- and *K*-selected
      d. not selected

   Solution:

   A

Exercise:

   Problem: A forest fire is an example of _____ regulation.

      a. density-dependent

b. density-independent
c. *r*-selected
d. *K*-selected

Solution:

B

Exercise:

Problem: Primates are examples of:

a. density-dependent species
b. density-independent species
c. *r*-selected species
d. *K*-selected species

Solution:

D

Free Response

Exercise:

Problem:

Give an example of how density-dependent and density-independent factors might interact.

Solution:

If a natural disaster such as a fire happened in the winter, when populations are low, it would have a greater effect on the overall population and its recovery than if the same disaster occurred during the summer, when population levels are high.

Glossary

demographic-based population model
   modern model of population dynamics incorporating many features of
   the *r*- and *K*-selection theory

density-dependent regulation
   regulation of population that is influenced by population density, such
   as crowding effects; usually involves biotic factors

density-independent regulation
   regulation of populations by factors that operate independent of
   population density, such as forest fires and volcanic eruptions; usually
   involves abiotic factors

interspecific competition
   competition between species for resources in a shared habitat or
   environment

K-selected species
   species suited to stable environments that produce a few, relatively
   large offspring and provide parental care

r-selected species
   species suited to changing environments that produce many offspring
   and provide little or no parental care

Community Ecology
By the end of this section, you will be able to:

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Describe community structure and succession

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations inhabiting a specific area at the same time. The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

Predation and Herbivory

Perhaps the classical example of species interaction is predation: the hunting of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests ([link]). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx

population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.

Predator-prey Dynamics
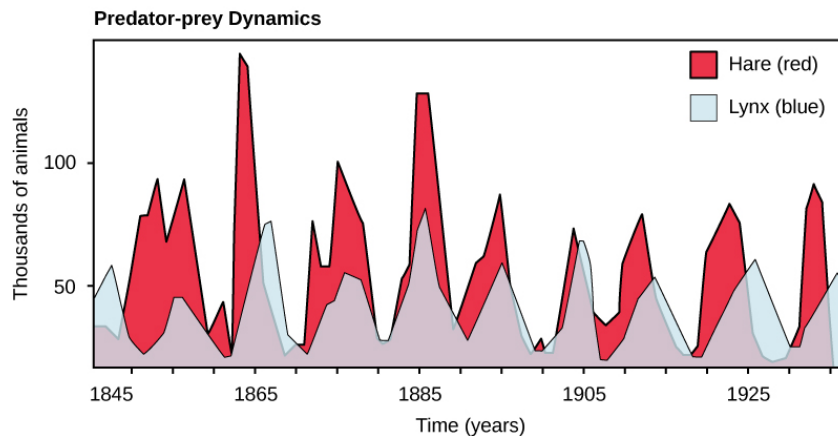
The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

The idea that the population cycling of the two species is entirely controlled by predation models has come under question. More recent studies have pointed to undefined density-dependent factors as being important in the cycling, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for

example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. [link] shows some organisms' defenses against predation and herbivory.

The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni)* uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs ([link]**a**). In another example, the chameleon can change its color to match its surroundings ([link]**b**). Both of these are examples of **camouflage**, or avoiding detection by blending in with the background.

(a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemical, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called **aposematic coloration**, or warning coloration ([link]).

(a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In **Batesian mimicry**, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation ([link]).

Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)

In **Müllerian mimicry**, multiple species share the same warning coloration, but all of them actually have defenses. [link] shows a variety of foul-tasting butterflies with similar coloration. In **Emsleyan/Mertensian mimicry**, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the non-venomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.

Several unpleasant-tasting *Heliconius* butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Note:
Link to Learning

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The **competitive exclusion principle** states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in [link], with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.
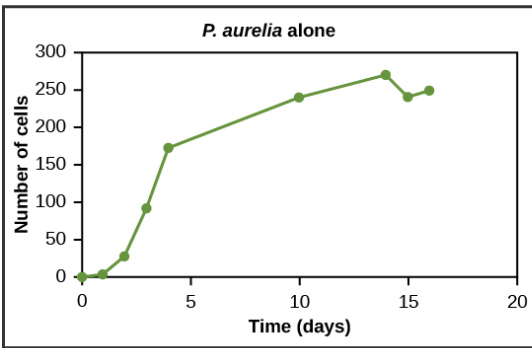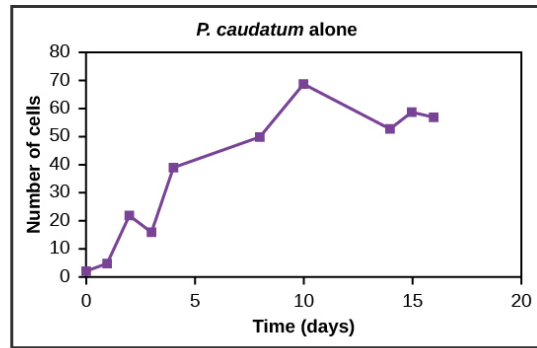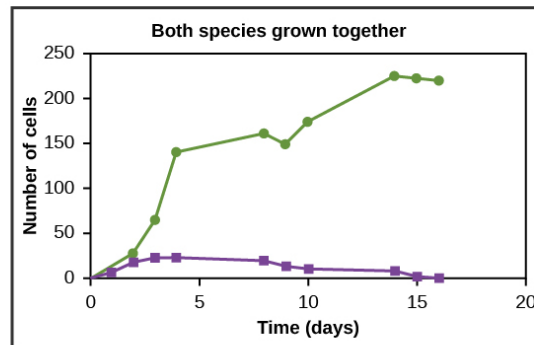
Paramecium aurelia and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These organisms coexist by minimizing direct competition.

Symbiosis

Symbiotic relationships, or **symbioses** (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only

those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

Commensalism

A **commensal** relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship ([link]). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.

The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley,

Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: "Hanay"/Wikimedia Commons)

Mutualism

A second type of symbiotic relationship is called **mutualism**, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect's gut ([link]**a**). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria ([link]**b**). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.

(a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Parasitism

A **parasite** is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the organism being fed upon, the **host** is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed ([link]). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle,

making two hosts necessary to complete its life cycle. Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.

Tapeworm *(Taenia)* **Infection**

3 Tapeworm embryos hatch, penetrate the intestinal wall, and circulate to musculature in pigs or humans.

Embryos develop into larvae in muscles of pigs or humans.

Cysts may develop in any organ, and are most common in subcutaneous tissue as well as in the brain and eyes.

Humans acquire the infection by ingesting **4** raw or undercooked meat from an infected animal host.

2 Eggs or segments are ingested by pigs or humans.

5 The tapeworm attaches itself to the intestine via hooks on the scolex.

Scolex

1 Eggs or tapeworm segments in feces are passed into the environment.

6 Adults in small intestine

This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how

communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

Foundation species are considered the "base" or "bedrock" of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef ([link]). Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.
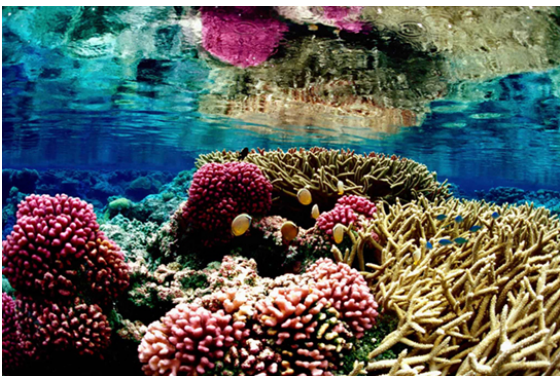
Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS)

Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. **Species richness** is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe ([link]). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of **island biogeography** attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. **Relative species abundance** is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.
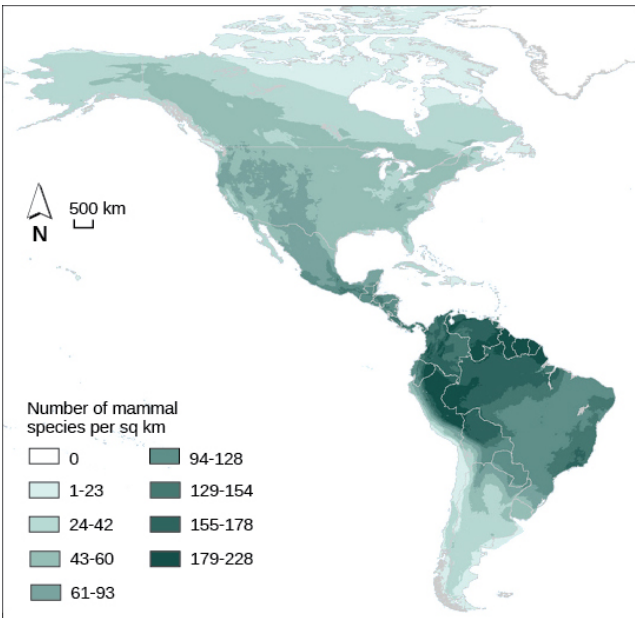
The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

Keystone Species

A **keystone species** is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species ([link]). Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If

these fish were to become extinct, the community would be greatly affected.

The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by **environmental disturbances** such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In **primary succession**, newly exposed or newly formed land is colonized by living things; in **secondary succession**, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as **pioneer species** ([link]). These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.

During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire ([link]). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate

species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the **climax community**, which will remain stable until the next disturbance.

Secondary Succession of an Oak and Hickory Forest

Pioneer species
Annual plants grow and are succeeded by grasses and perennials.

Intermediate species
Shrubs, then pines, and young oak and hickory begin to grow.

Climax community
The mature oak and hickory forest remains stable until the next disturbance.
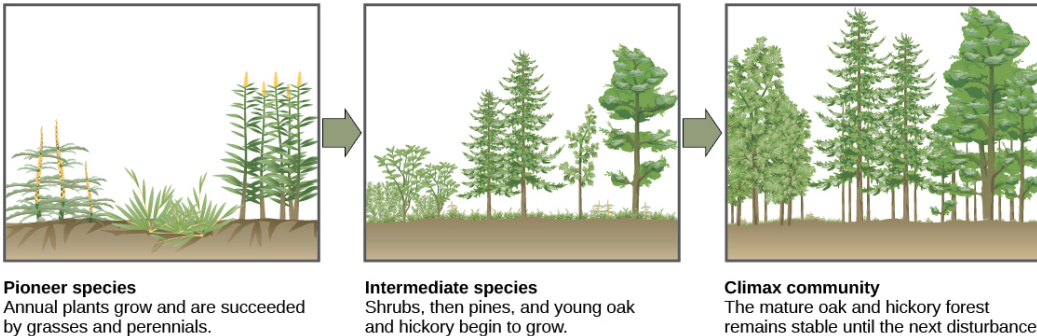
Secondary succession is shown in an oak and hickory forest after a forest fire.

Section Summary

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism. Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established.

Review Questions

Exercise:

Problem:

The first species to live on new land, such as that formed from volcanic lava, are called _____.

   a. climax community
   b. keystone species
   c. foundation species
   d. pioneer species

Solution:

D

Exercise:

Problem:

Which type of mimicry involves multiple species with similar warning coloration that are all toxic to predators?

   a. Batesian mimicry
   b. Müllerian mimicry
   c. Emsleyan/Mertensian mimicry
   d. Mertensian mimicry

Solution:

B

Exercise:

Problem:

A symbiotic relationship where both of the coexisting species benefit from the interaction is called _____.

a. commensalism
b. parasitism
c. mutualism
d. communism

Solution:

C

Free Response

Exercise:

Problem:

Describe the competitive exclusion principle and its effects on competing species.

Solution:

The competitive exclusion principle states that no two species competing for the same resources at the same time and place can coexist over time. Thus, one of the competing species will eventually dominate. On the other hand, if the species evolve such that they use resources from different parts of the habitat or at different times of day, the two species can exist together indefinitely.

Glossary

aposematic coloration
    warning coloration used as a defensive mechanism against predation

Batesian mimicry
    type of mimicry where a non-harmful species takes on the warning colorations of a harmful one

camouflage
    avoid detection by blending in with the background.

climax community
    final stage of succession, where a stable community is formed by a
    characteristic assortment of plant and animal species

commensalism
    relationship between species wherein one species benefits from the
    close, prolonged interaction, while the other species neither benefits
    nor is harmed

competitive exclusion principle
    no two species within a habitat can coexist when they compete for the
    same resources at the same place and time

Emsleyan/Mertensian mimicry
    type of mimicry where a harmful species resembles a less harmful one

environmental disturbance
    change in the environment caused by natural disasters or human
    activities

foundation species
    species which often forms the major structural portion of the habitat

host
    organism a parasite lives on

island biogeography
    study of life on island chains and how their geography interacts with
    the diversity of species found there

keystone species
    species whose presence is key to maintaining biodiversity in an
    ecosystem and to upholding an ecological community's structure

Müllerian mimicry

type of mimicry where species share warning coloration and all are harmful to predators

mutualism
      symbiotic relationship between two species where both species benefit

parasite
      organism that uses resources from another species, the host

pioneer species
      first species to appear in primary and secondary succession

primary succession
      succession on land that previously has had no life

relative species abundance
      absolute population size of a particular species relative to the population sizes of other species within the community

secondary succession
      succession in response to environmental disturbances that move a community away from its equilibrium

species richness
      number of different species in a community

symbiosis
      close interaction between individuals of different species over an extended period of time that impacts the abundance and distribution of the associating populations

Introduction
class="introduction"

In the southwestern United States, rainy weather causes an increase in production of pinyon nuts, causing the deer mouse population to explode. Deer mice may carry a virus called *Sin Nombre* (a hantavirus) that causes respiratory disease in humans and has a high fatality rate. In 1992–1993, wet *El Niño* weather caused a *Sin Nombre* epidemic. Navajo

healers, who were aware of the link between this disease and weather, predicted the outbreak. (credit "highway": modification of work by Phillip Capper; credit "mouse": modification of work by USFWS)

In 1993, an interesting example of ecosystem dynamics occurred when a rare lung disease struck inhabitants of the southwestern United States. This disease had an alarming rate of fatalities, killing more than half of early patients, many of whom were Native Americans. These formerly healthy

young adults died from complete respiratory failure. The disease was unknown, and the Centers for Disease Control (CDC), the United States government agency responsible for managing potential epidemics, was brought in to investigate. The scientists could have learned about the disease had they known to talk with the Navajo healers who lived in the area and who had observed the connection between rainfall and mice populations, thereby predicting the 1993 outbreak.

The cause of the disease, determined within a few weeks by the CDC investigators, was the hantavirus known as *Sin Nombre*, the virus with "no name." With insights from traditional Navajo medicine, scientists were able to characterize the disease rapidly and institute effective health measures to prevent its spread. This example illustrates the importance of understanding the complexities of ecosystems and how they respond to changes in the environment.

Ecology of Ecosystems
By the end of this section, you will be able to:

- Describe the basic types of ecosystems on Earth
- Explain the methods that ecologists use to study ecosystem structure and dynamics
- Identify the different methods of ecosystem modeling
- Differentiate between food chains and food webs and recognize the importance of each

Life in an ecosystem is often about competition for limited resources, a characteristic of the theory of natural selection. Competition in communities (all living things within specific habitats) is observed both within species and among different species. The resources for which organisms compete include organic material from living or previously living organisms, sunlight, and mineral nutrients, which provide the energy for living processes and the matter to make up organisms' physical structures. Other critical factors influencing community dynamics are the components of its physical and geographic environment: a habitat's latitude, amount of rainfall, topography (elevation), and available species. These are all important environmental variables that determine which organisms can exist within a particular area.

An **ecosystem** is a community of living organisms and their interactions with their abiotic (non-living) environment. Ecosystems can be small, such as the tide pools found near the rocky shores of many oceans, or large, such as the Amazon Rainforest in Brazil ([link]).

(a)   (b)

A (a) tidal pool ecosystem in Matinicus Island in Maine is a small ecosystem, while the (b) Amazon Rainforest in Brazil is a large ecosystem. (credit a: modification of work by "takomabibelot"/Flickr; credit b: modification of work by Ivan Mlinaric)

There are three broad categories of ecosystems based on their general environment: freshwater, ocean water, and terrestrial. Within these broad categories are individual ecosystem types based on the organisms present and the type of environmental habitat.

Ocean ecosystems are the most common, comprising 75 percent of the Earth's surface and consisting of three basic types: shallow ocean, deep ocean water, and deep ocean surfaces (the low depth areas of the deep oceans). The shallow ocean ecosystems include extremely biodiverse coral reef ecosystems, and the deep ocean surface is known for its large numbers of plankton and krill (small crustaceans) that support it. These two environments are especially important to aerobic respirators worldwide as the phytoplankton perform 40 percent of all photosynthesis on Earth. Although not as diverse as the other two, deep ocean ecosystems contain a wide variety of marine organisms. Such ecosystems exist even at the bottom of the ocean where light is unable to penetrate through the water.

Freshwater ecosystems are the rarest, occurring on only 1.8 percent of the Earth's surface. Lakes, rivers, streams, and springs comprise these systems; they are quite diverse, and they support a variety of fish, amphibians, reptiles, insects, phytoplankton, fungi, and bacteria.

Terrestrial ecosystems, also known for their diversity, are grouped into large categories called biomes, such as tropical rain forests, savannas, deserts, coniferous forests, deciduous forests, and tundra. Grouping these ecosystems into just a few biome categories obscures the great diversity of the individual ecosystems within them. For example, there is great variation in desert vegetation: the saguaro cacti and other plant life in the Sonoran Desert, in the United States, are relatively abundant compared to the

desolate rocky desert of Boa Vista, an island off the coast of Western Africa ([link]).

(a)

(b)

Desert ecosystems, like all ecosystems, can vary greatly. The desert in (a) Saguaro National Park, Arizona, has abundant plant life, while the rocky desert of (b) Boa Vista island, Cape Verde, Africa, is devoid of plant life. (credit a: modification of work by Jay Galvin; credit b: modification of work by Ingo Wölbern)

Ecosystems are complex with many interacting parts. They are routinely exposed to various disturbances, or changes in the environment that effect their compositions: yearly variations in rainfall and temperature and the slower processes of plant growth, which may take several years. Many of these disturbances are a result of natural processes. For example, when lightning causes a forest fire and destroys part of a forest ecosystem, the ground is eventually populated by grasses, then by bushes and shrubs, and later by mature trees, restoring the forest to its former state. The impact of environmental disturbances caused by human activities is as important as the changes wrought by natural processes. Human agricultural practices, air pollution, acid rain, global deforestation, overfishing, eutrophication, oil spills, and illegal dumping on land and into the ocean are all issues of concern to conservationists.

Equilibrium is the steady state of an ecosystem where all organisms are in balance with their environment and with each other. In ecology, two

parameters are used to measure changes in ecosystems: resistance and resilience. The ability of an ecosystem to remain at equilibrium in spite of disturbances is called **resistance**. The speed at which an ecosystem recovers equilibrium after being disturbed, called its **resilience**. Ecosystem resistance and resilience are especially important when considering human impact. The nature of an ecosystem may change to such a degree that it can lose its resilience entirely. This process can lead to the complete destruction or irreversible altering of the ecosystem.

Food Chains and Food Webs

The term "food chain" is sometimes used metaphorically to describe human social situations. In this sense, food chains are thought of as a competition for survival, such as "who eats whom?" Someone eats and someone is eaten. Therefore, it is not surprising that in our competitive "dog-eat-dog" society, individuals who are considered successful are seen as being at the top of the food chain, consuming all others for their benefit, whereas the less successful are seen as being at the bottom.

The scientific understanding of a food chain is more precise than in its everyday usage. In ecology, a **food chain** is a linear sequence of organisms through which nutrients and energy pass: primary producers, primary consumers, and higher-level consumers are used to describe ecosystem structure and dynamics. There is a single path through the chain. Each organism in a food chain occupies what is called a **trophic level**. Depending on their role as producers or consumers, species or groups of species can be assigned to various trophic levels.

In many ecosystems, the bottom of the food chain consists of photosynthetic organisms (plants and/or phytoplankton), which are called **primary producers**. The organisms that consume the primary producers are herbivores: the **primary consumers**. **Secondary consumers** are usually carnivores that eat the primary consumers. **Tertiary consumers** are carnivores that eat other carnivores. Higher-level consumers feed on the next lower tropic levels, and so on, up to the organisms at the top of the food chain: the **apex consumers**. In the Lake Ontario food chain shown in

[link], the Chinook salmon is the apex consumer at the top of this food chain.
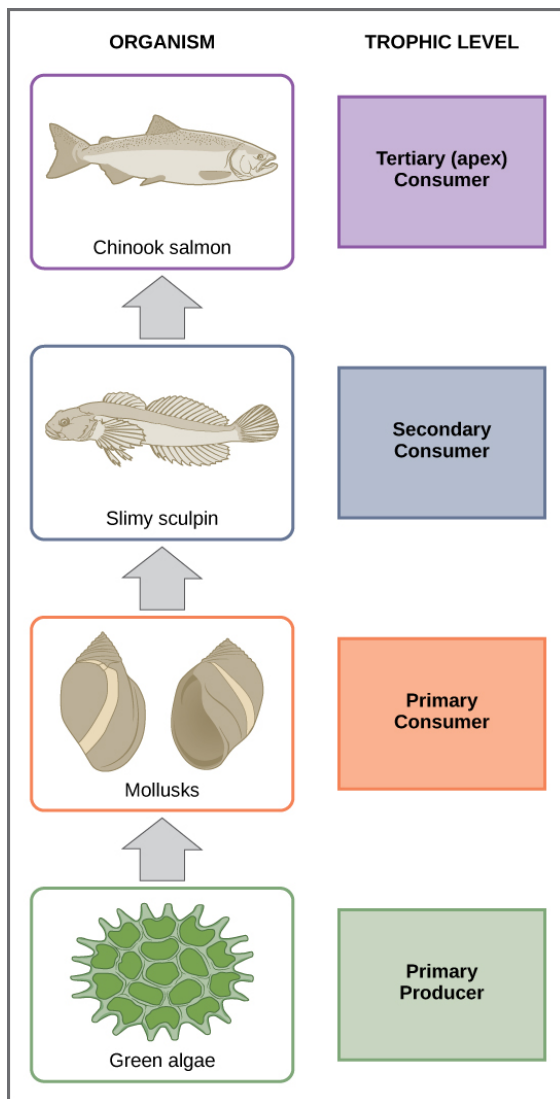
These are the trophic levels of a food chain in Lake Ontario at the United States-Canada border. Energy and nutrients flow from photosynthetic green algae at the bottom to the top of the

food chain: the Chinook
salmon.

One major factor that limits the length of food chains is energy. Energy is lost as heat between each trophic level due to the second law of thermodynamics. Thus, after a limited number of trophic energy transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at yet a higher trophic level.

The loss of energy between trophic levels is illustrated by the pioneering studies of Howard T. Odum in the Silver Springs, Florida, ecosystem in the 1940s ([link]). The primary producers generated 20,819 kcal/m^2/yr (kilocalories per square meter per year), the primary consumers generated 3368 kcal/m^2/yr, the secondary consumers generated 383 kcal/m^2/yr, and the tertiary consumers only generated 21 kcal/m^2/yr. Thus, there is little energy remaining for another level of consumers in this ecosystem.
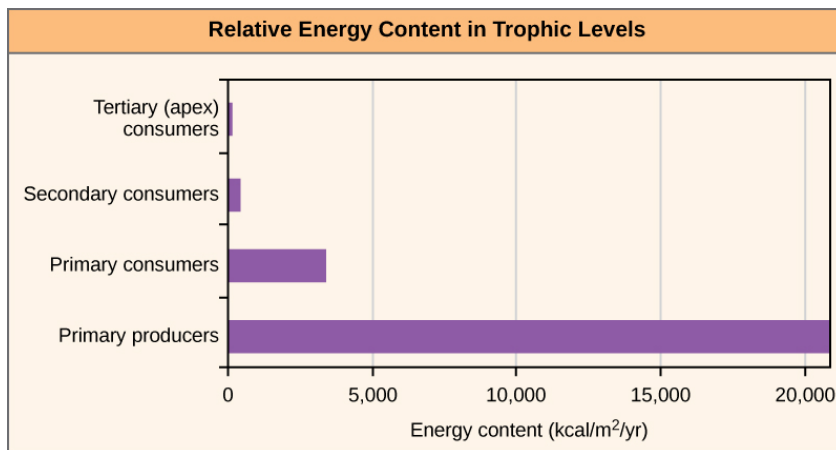
The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available and supports fewer organisms at the next level.

There is a one problem when using food chains to accurately describe most ecosystems. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed on species from more than one trophic level; likewise, some of these organisms can be eaten by species from multiple trophic levels. In other words, the linear model of ecosystems, the food chain, is not completely descriptive of ecosystem structure. A holistic model—which accounts for all the interactions between different species and their complex interconnected relationships with each other and with the environment—is a more accurate and descriptive model for ecosystems. A **food web** is a graphic representation of a holistic, non-linear web of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics ([link]).
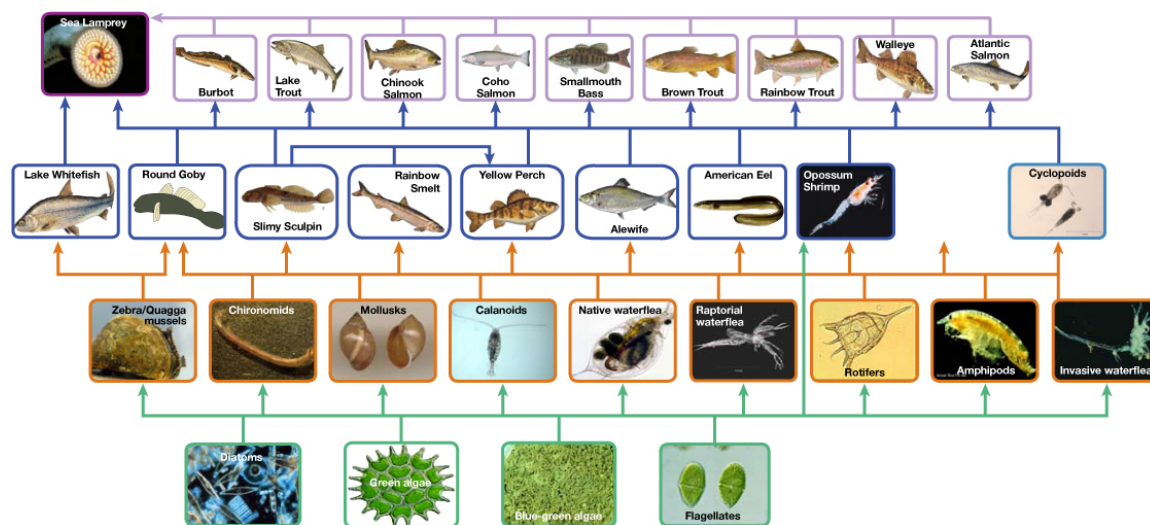
This food web shows the interactions between organisms across trophic levels in the Lake Ontario ecosystem. Primary producers are outlined in green, primary consumers in orange, secondary consumers in blue, and tertiary (apex) consumers in purple. Arrows point from an organism that is consumed to the organism that consumes it. Notice how some lines point to more than one trophic level. For example, the opossum shrimp eats both primary producers and primary consumers. (credit: NOAA, GLERL)

A comparison of the two types of structural ecosystem models shows strength in both. Food chains are more flexible for analytical modeling, are easier to follow, and are easier to experiment with, whereas food web models more accurately represent ecosystem structure and dynamics, and data can be directly used as input for simulation modeling.

Two general types of food webs are often shown interacting within a single ecosystem. A **grazing food web** (such as the Lake Ontario food web in [link]) has plants or other photosynthetic organisms at its base, followed by herbivores and various carnivores. A **detrital food web** consists of a base of organisms that feed on decaying organic matter (dead organisms), called decomposers or detritivores. These organisms are usually bacteria or fungi that recycle organic material back into the biotic part of the ecosystem as they themselves are consumed by other organisms. As all ecosystems require a method to recycle material from dead organisms, most grazing food webs have an associated detrital food web. For example, in a meadow ecosystem, plants may support a grazing food web of different organisms, primary and other levels of consumers, while at the same time supporting a

detrital food web of bacteria, fungi, and detrivorous invertebrates feeding off dead plants and animals.

Note:
Evolution Conenction
Three-spined Stickleback
It is well established by the theory of natural selection that changes in the environment play a major role in the evolution of species within an ecosystem. However, little is known about how the evolution of species within an ecosystem can alter the ecosystem environment. In 2009, Dr. Luke Harmon, from the University of Idaho in Moscow, published a paper that for the first time showed that the evolution of organisms into subspecies can have direct effects on their ecosystem environment.[footnote] *Nature* (Vol. 458, April 1, 2009)

The three-spines stickleback (*Gasterosteus aculeatus*) is a freshwater fish that evolved from a saltwater fish to live in freshwater lakes about 10,000 years ago, which is considered a recent development in evolutionary time ([link]). Over the last 10,000 years, these freshwater fish then became isolated from each other in different lakes. Depending on which lake population was studied, findings showed that these sticklebacks then either remained as one species or evolved into two species. The divergence of species was made possible by their use of different areas of the pond for feeding called micro niches.

Dr. Harmon and his team created artificial pond microcosms in 250-gallon tanks and added muck from freshwater ponds as a source of zooplankton and other invertebrates to sustain the fish. In different experimental tanks they introduced one species of stickleback from either a single-species or double-species lake.

Over time, the team observed that some of the tanks bloomed with algae while others did not. This puzzled the scientists, and they decided to measure the water's dissolved organic carbon (DOC), which consists of mostly large molecules of decaying organic matter that give pond-water its slightly brownish color. It turned out that the water from the tanks with two-species fish contained larger particles of DOC (and hence darker water) than water with single-species fish. This increase in DOC blocked

the sunlight and prevented algal blooming. Conversely, the water from the single-species tank contained smaller DOC particles, allowing more sunlight penetration to fuel the algal blooms.

This change in the environment, which is due to the different feeding habits of the stickleback species in each lake type, probably has a great impact on the survival of other species in these ecosystems, especially other photosynthetic organisms. Thus, the study shows that, at least in these ecosystems, the environment and the evolution of populations have reciprocal effects that may now be factored into simulation models.

The three-spined stickleback evolved from a saltwater fish to freshwater fish. (credit: Barrett Paul, USFWS)

Research into Ecosystem Dynamics: Ecosystem Experimentation and Modeling

The study of the changes in ecosystem structure caused by changes in the environment (disturbances) or by internal forces is called **ecosystem dynamics**. Ecosystems are characterized using a variety of research methodologies. Some ecologists study ecosystems using controlled experimental systems, while some study entire ecosystems in their natural state, and others use both approaches.

A **holistic ecosystem model** attempts to quantify the composition, interaction, and dynamics of entire ecosystems; it is the most representative of the ecosystem in its natural state. A food web is an example of a holistic ecosystem model. However, this type of study is limited by time and expense, as well as the fact that it is neither feasible nor ethical to do experiments on large natural ecosystems. To quantify all different species in an ecosystem and the dynamics in their habitat is difficult, especially when studying large habitats such as the Amazon Rainforest, which covers 1.4 billion acres (5.5 million km^2) of the Earth's surface.

For these reasons, scientists study ecosystems under more controlled conditions. Experimental systems usually involve either partitioning a part of a natural ecosystem that can be used for experiments, termed a **mesocosm**, or by re-creating an ecosystem entirely in an indoor or outdoor laboratory environment, which is referred to as a **microcosm**. A major limitation to these approaches is that removing individual organisms from their natural ecosystem or altering a natural ecosystem through partitioning may change the dynamics of the ecosystem. These changes are often due to differences in species numbers and diversity and also to environment alterations caused by partitioning (mesocosm) or re-creating (microcosm) the natural habitat. Thus, these types of experiments are not totally predictive of changes that would occur in the ecosystem from which they were gathered.

As both of these approaches have their limitations, some ecologists suggest that results from these experimental systems should be used only in conjunction with holistic ecosystem studies to obtain the most representative data about ecosystem structure, function, and dynamics.

Scientists use the data generated by these experimental studies to develop ecosystem models that demonstrate the structure and dynamics of ecosystems. Three basic types of ecosystem modeling are routinely used in research and ecosystem management: a conceptual model, an analytical model, and a simulation model. A **conceptual model** is an ecosystem model that consists of flow charts to show interactions of different compartments of the living and nonliving components of the ecosystem. A conceptual model describes ecosystem structure and dynamics and shows

how environmental disturbances affect the ecosystem; however, its ability to predict the effects of these disturbances is limited. Analytical and simulation models, in contrast, are mathematical methods of describing ecosystems that are indeed capable of predicting the effects of potential environmental changes without direct experimentation, although with some limitations as to accuracy. An **analytical model** is an ecosystem model that is created using simple mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and dynamics. A **simulation model** is an ecosystem model that is created using complex computer algorithms to holistically model ecosystems and to predict the effects of environmental disturbances on ecosystem structure and dynamics. Ideally, these models are accurate enough to determine which components of the ecosystem are particularly sensitive to disturbances, and they can serve as a guide to ecosystem managers (such as conservation ecologists or fisheries biologists) in the practical maintenance of ecosystem health.

Conceptual Models

Conceptual models are useful for describing ecosystem structure and dynamics and for demonstrating the relationships between different organisms in a community and their environment. Conceptual models are usually depicted graphically as flow charts. The organisms and their resources are grouped into specific compartments with arrows showing the relationship and transfer of energy or nutrients between them. Thus, these diagrams are sometimes called compartment models.

To model the cycling of mineral nutrients, organic and inorganic nutrients are subdivided into those that are bioavailable (ready to be incorporated into biological macromolecules) and those that are not. For example, in a terrestrial ecosystem near a deposit of coal, carbon will be available to the plants of this ecosystem as carbon dioxide gas in a short-term period, not from the carbon-rich coal itself. However, over a longer period, microorganisms capable of digesting coal will incorporate its carbon or release it as natural gas (methane, CH_4), changing this unavailable organic source into an available one. This conversion is greatly accelerated by the combustion of fossil fuels by humans, which releases large amounts of

carbon dioxide into the atmosphere. This is thought to be a major factor in the rise of the atmospheric carbon dioxide levels in the industrial age. The carbon dioxide released from burning fossil fuels is produced faster than photosynthetic organisms can use it. This process is intensified by the reduction of photosynthetic trees because of worldwide deforestation. Most scientists agree that high atmospheric carbon dioxide is a major cause of global climate change.

Conceptual models are also used to show the flow of energy through particular ecosystems. [link] is based on Howard T. Odum's classical study of the Silver Springs, Florida, holistic ecosystem in the mid-twentieth century.[footnote] This study shows the energy content and transfer between various ecosystem compartments.
Howard T. Odum, "Trophic Structure and Productivity of Silver Springs, Florida," *Ecological Monographs* 27, no. 1 (1957): 47–112.

Note:
Art Connection
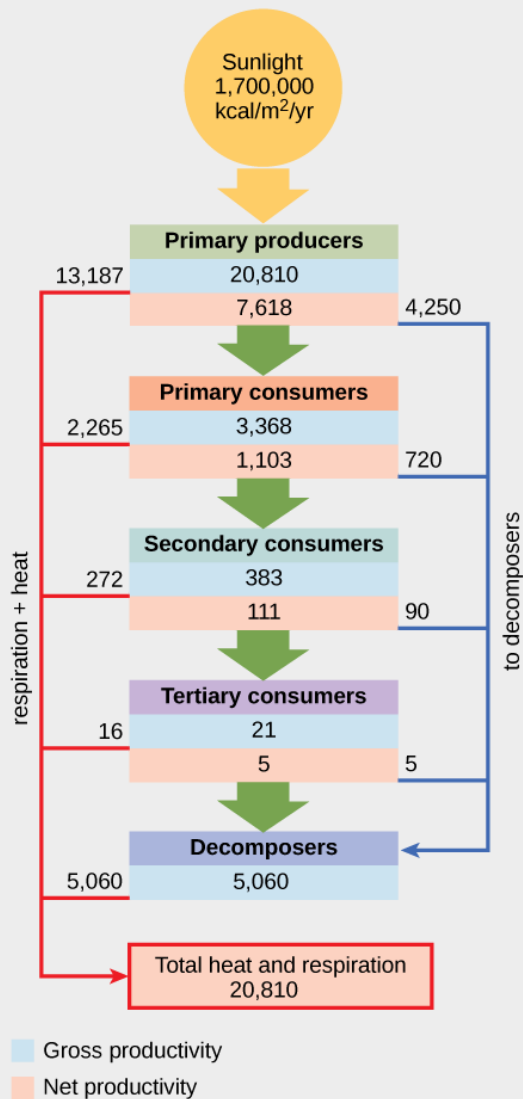
This conceptual model shows the flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic level.

Why do you think the value for gross productivity of the primary producers is the same as the value for total heat and respiration (20,810 kcal/m^2/yr)?

Analytical and Simulation Models

The major limitation of conceptual models is their inability to predict the consequences of changes in ecosystem species and/or environment. Ecosystems are dynamic entities and subject to a variety of abiotic and biotic disturbances caused by natural forces and/or human activity. Ecosystems altered from their initial equilibrium state can often recover from such disturbances and return to a state of equilibrium. As most ecosystems are subject to periodic disturbances and are often in a state of change, they are usually either moving toward or away from their equilibrium state. There are many of these equilibrium states among the various components of an ecosystem, which affects the ecosystem overall. Furthermore, as humans have the ability to greatly and rapidly alter the species content and habitat of an ecosystem, the need for predictive models that enable understanding of how ecosystems respond to these changes becomes more crucial.

Analytical models often use simple, linear components of ecosystems, such as food chains, and are known to be complex mathematically; therefore, they require a significant amount of mathematical knowledge and expertise. Although analytical models have great potential, their simplification of complex ecosystems is thought to limit their accuracy. Simulation models that use computer programs are better able to deal with the complexities of ecosystem structure.

A recent development in simulation modeling uses supercomputers to create and run individual-based simulations, which accounts for the behavior of individual organisms and their effects on the ecosystem as a whole. These simulations are considered to be the most accurate and predictive of the complex responses of ecosystems to disturbances.

Note:
Link to Learning

Visit [The Darwin Project](#) to view a variety of ecosystem models.

Section Summary

Ecosystems exist on land, at sea, in the air, and underground. Different ways of modeling ecosystems are necessary to understand how environmental disturbances will affect ecosystem structure and dynamics. Conceptual models are useful to show the general relationships between organisms and the flow of materials or energy between them. Analytical models are used to describe linear food chains, and simulation models work best with holistic food webs.

Art Connections

Exercise:

Problem:

[link] Why do you think the value for gross productivity of the primary producers is the same as the value for total heat and respiration (20,810 kcal/m^2/yr)?

Solution:

[link] According to the first law of thermodynamics, energy can neither be created nor destroyed. Eventually, all energy consumed by living systems is lost as heat or used for respiration, and the total energy output of the system must equal the energy that went into it.

Review Questions

Exercise:

Problem:

The ability of an ecosystem to return to its equilibrium state after an environmental disturbance is called _____.

   a. resistance
   b. restoration
   c. reformation
   d. resilience

Solution:

D

Exercise:

Problem:

A re-created ecosystem in a laboratory environment is known as a _____.

   a. mesocosm
   b. simulation
   c. microcosm
   d. reproduction

Solution:

C

Exercise:

Problem: Decomposers are associated with which class of food web?

a. grazing
b. detrital
c. inverted
d. aquatic

Solution:

B

Exercise:

Problem:

The primary producers in an ocean grazing food web are usually
_____.

a. plants
b. animals
c. fungi
d. phytoplankton

Solution:

D

Exercise:

Problem:

What term describes the use of mathematical equations in the modeling of linear aspects of ecosystems?

a. analytical modeling
b. simulation modeling
c. conceptual modeling
d. individual-based modeling

Solution:

A
Exercise:

Problem:

The position of an organism along a food chain is known as its
_____.

    a. locus
    b. location
    c. trophic level
    d. microcosm

Solution:

C

Free Response

Exercise:

Problem:

Compare and contrast food chains and food webs. What are the
strengths of each concept in describing ecosystems?

Solution:

Food webs show interacting groups of different species and their many
interconnections with each other and the environment. Food chains are
linear aspects of food webs that describe the succession of organisms
consuming one another at defined trophic levels. Food webs are a
more accurate representation of the structure and dynamics of an
ecosystem. Food chains are easier to model and use for experimental
studies.

Exercise:

Problem: Describe freshwater, ocean, and terrestrial ecosystems.

Solution:

Freshwater ecosystems are the rarest, but have great diversity of freshwater fish and other aquatic life. Ocean ecosystems are the most common and are responsible for much of the photosynthesis that occurs on Earth. Terrestrial ecosystems are very diverse; they are grouped based on their species and environment (biome), which includes forests, deserts, and tundras.

Exercise:

Problem:

Compare grazing and detrital food webs. Why would they both be present in the same ecosystem?

Solution:

Grazing food webs have a primary producer at their base, which is either a plant for terrestrial ecosystems or a phytoplankton for aquatic ecosystems. The producers pass their energy to the various trophic levels of consumers. At the base of detrital food webs are the decomposers, which pass this energy to a variety of other consumers. Detrital food webs are important for the health of many grazing food webs because they eliminate dead and decaying organic material, thus, clearing space for new organisms and removing potential causes of disease. By breaking down dead organic matter, decomposers also make mineral nutrients available to primary producers; this process is a vital link in nutrient cycling.

Glossary

analytical model
    ecosystem model that is created with mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and

dynamics

apex consumer
    organism at the top of the food chain

conceptual model
    (also, compartment models) ecosystem model that consists of flow
    charts that show the interactions of different compartments of the
    living and non-living components of the ecosystem

detrital food web
    type of food web in which the primary consumers consist of
    decomposers; these are often associated with grazing food webs within
    the same ecosystem

ecosystem
    community of living organisms and their interactions with their abiotic
    environment

ecosystem dynamics
    study of the changes in ecosystem structure caused by changes in the
    environment or internal forces

equilibrium
    steady state of an ecosystem where all organisms are in balance with
    their environment and each other

food chain
    linear representation of a chain of primary producers, primary
    consumers, and higher-level consumers used to describe ecosystem
    structure and dynamics

food web
    graphic representation of a holistic, non-linear web of primary
    producers, primary consumers, and higher-level consumers used to
    describe ecosystem structure and dynamics

grazing food web

type of food web in which the primary producers are either plants on land or phytoplankton in the water; often associated with a detrital food web within the same ecosystem

holistic ecosystem model
    study that attempts to quantify the composition, interactions, and dynamics of entire ecosystems; often limited by economic and logistical difficulties, depending on the ecosystem

mesocosm
    portion of a natural ecosystem to be used for experiments

microcosm
    re-creation of natural ecosystems entirely in a laboratory environment to be used for experiments

primary consumer
    trophic level that obtains its energy from the primary producers of an ecosystem

primary producer
    trophic level that obtains its energy from sunlight, inorganic chemicals, or dead and/or decaying organic material

resilience (ecological)
    speed at which an ecosystem recovers equilibrium after being disturbed

resistance (ecological)
    ability of an ecosystem to remain at equilibrium in spite of disturbances

secondary consumer
    usually a carnivore that eat primary consumers

simulation model
    ecosystem model that is created with computer programs to holistically model ecosystems and to predict the effects of environmental

disturbances on ecosystem structure and dynamics

tertiary consumer
    carnivore that eat other carnivores

trophic level
    position of a species or group of species in a food chain or a food web

Energy Flow through Ecosystems
By the end of this section, you will be able to:

- Describe how organisms acquire energy in a food web and in associated food chains
- Explain how the efficiency of energy transfers between trophic levels affects ecosystem structure and dynamics
- Discuss trophic levels and how ecological pyramids are used to model them

All living things require energy in one form or another. Energy is required by most complex metabolic pathways (often in the form of adenosine triphosphate, ATP), especially those responsible for building large molecules from smaller compounds, and life itself is an energy-driven process. Living organisms would not be able to assemble macromolecules (proteins, lipids, nucleic acids, and complex carbohydrates) from their monomeric subunits without a constant energy input.

It is important to understand how organisms acquire energy and how that energy is passed from one organism to another through food webs and their constituent food chains. Food webs illustrate how energy flows directionally through ecosystems, including how efficiently organisms acquire it, use it, and how much remains for use by other organisms of the food web.

How Organisms Acquire Energy in a Food Web

Energy is acquired by living things in three ways: photosynthesis, chemosynthesis, and the consumption and digestion of other living or previously living organisms by heterotrophs.

Photosynthetic and chemosynthetic organisms are both grouped into a category known as autotrophs: organisms capable of synthesizing their own food (more specifically, capable of using inorganic carbon as a carbon source). Photosynthetic autotrophs (photoautotrophs) use sunlight as an energy source, whereas chemosynthetic autotrophs (chemoautotrophs) use inorganic molecules as an energy source. Autotrophs are critical for all

ecosystems. Without these organisms, energy would not be available to other living organisms and life itself would not be possible.

Photoautotrophs, such as plants, algae, and photosynthetic bacteria, serve as the energy source for a majority of the world's ecosystems. These ecosystems are often described by grazing food webs. Photoautotrophs harness the solar energy of the sun by converting it to chemical energy in the form of ATP (and NADP). The energy stored in ATP is used to synthesize complex organic molecules, such as glucose.

Chemoautotrophs are primarily bacteria that are found in rare ecosystems where sunlight is not available, such as in those associated with dark caves or hydrothermal vents at the bottom of the ocean ([link]). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H_2S), which is released from the vents as a source of chemical energy. This allows chemoautotrophs to synthesize complex organic molecules, such as glucose, for their own energy and in turn supplies energy to the rest of the ecosystem.

Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the

ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture was taken in 2006 at the submerged NW Eifuku volcano off the coast of Japan by the National Oceanic and Atmospheric Administration (NOAA). The summit of this highly active volcano lies 1535 m below the surface.

Productivity within Trophic Levels

Productivity within an ecosystem can be defined as the percentage of energy entering the ecosystem incorporated into biomass in a particular trophic level. **Biomass** is the total mass, in a unit area at the time of measurement, of living or previously living organisms within a trophic level. Ecosystems have characteristic amounts of biomass at each trophic level. For example, in the English Channel ecosystem the primary producers account for a biomass of 4 g/m^2 (grams per meter squared), while the primary consumers exhibit a biomass of 21 g/m^2.

The productivity of the primary producers is especially important in any ecosystem because these organisms bring energy to other living organisms by photoautotrophy or chemoautotrophy. The rate at which photosynthetic primary producers incorporate energy from the sun is called **gross primary productivity**. An example of gross primary productivity is shown in the compartment diagram of energy flow within the Silver Springs aquatic ecosystem as shown ([link]). In this ecosystem, the total energy accumulated by the primary producers (gross primary productivity) was shown to be 20,810 $kcal/m^2/yr$.

Because all organisms need to use some of this energy for their own functions (like respiration and resulting metabolic heat loss) scientists often

refer to the net primary productivity of an ecosystem. **Net primary productivity** is the energy that remains in the primary producers after accounting for the organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level. In our Silver Spring example, 13,187 of the 20,810 kcal/m^2/yr were used for respiration or were lost as heat, leaving 7,632 kcal/m^2/yr of energy for use by the primary consumers.

Ecological Efficiency: The Transfer of Energy between Trophic Levels

As illustrated in [link], large amounts of energy are lost from the ecosystem from one trophic level to the next level as energy flows from the primary producers through the various trophic levels of consumers and decomposers. The main reason for this loss is the second law of thermodynamics, which states that whenever energy is converted from one form to another, there is a tendency toward disorder (entropy) in the system. In biologic systems, this means a great deal of energy is lost as metabolic heat when the organisms from one trophic level consume the next level. In the Silver Springs ecosystem example ([link]), we see that the primary consumers produced 1103 kcal/m^2/yr from the 7618 kcal/m^2/yr of energy available to them from the primary producers. The measurement of energy transfer efficiency between two successive trophic levels is termed the **trophic level transfer efficiency (TLTE)** and is defined by the formula:
Equation:

$$\text{TLTE} = \frac{\text{production at present trophic level}}{\text{production at previous trophic level}} \times 100$$

In Silver Springs, the TLTE between the first two trophic levels was approximately 14.8 percent. The low efficiency of energy transfer between trophic levels is usually the major factor that limits the length of food chains observed in a food web. The fact is, after four to six energy transfers, there is not enough energy left to support another trophic level. In the Lake Ontario example shown in [link], only three energy transfers occurred

between the primary producer, (green algae), and the apex consumer (Chinook salmon).

Ecologists have many different methods of measuring energy transfers within ecosystems. Some transfers are easier or more difficult to measure depending on the complexity of the ecosystem and how much access scientists have to observe the ecosystem. In other words, some ecosystems are more difficult to study than others, and sometimes the quantification of energy transfers has to be estimated.

Another main parameter that is important in characterizing energy flow within an ecosystem is the net production efficiency. **Net production efficiency (NPE)** allows ecologists to quantify how efficiently organisms of a particular trophic level incorporate the energy they receive into biomass; it is calculated using the following formula:
Equation:

$$\text{NPE} \ = \ \frac{\text{net consumer productivity}}{\text{assimilation}} \ \times \ 100$$

Net consumer productivity is the energy content available to the organisms of the next trophic level. **Assimilation** is the biomass (energy content generated per unit area) of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste. Incomplete ingestion refers to the fact that some consumers eat only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide.

Thus, NPE measures how efficiently each trophic level uses and incorporates the energy from its food into biomass to fuel the next trophic level. In general, cold-blooded animals (ectotherms), such as invertebrates, fish, amphibians, and reptiles, use less of the energy they obtain for respiration and heat than warm-blooded animals (endotherms), such as birds and mammals. The extra heat generated in endotherms, although an advantage in terms of the activity of these organisms in colder

environments, is a major disadvantage in terms of NPE. Therefore, many endotherms have to eat more often than ectotherms to get the energy they need for survival. In general, NPE for ectotherms is an order of magnitude (10x) higher than for endotherms. For example, the NPE for a caterpillar eating leaves has been measured at 18 percent, whereas the NPE for a squirrel eating acorns may be as low as 1.6 percent.

The inefficiency of energy use by warm-blooded animals has broad implications for the world's food supply. It is widely accepted that the meat industry uses large amounts of crops to feed livestock, and because the NPE is low, much of the energy from animal feed is lost. For example, it costs about 1¢ to produce 1000 dietary calories (kcal) of corn or soybeans, but approximately $0.19 to produce a similar number of calories growing cattle for beef consumption. The same energy content of milk from cattle is also costly, at approximately $0.16 per 1000 kcal. Much of this difference is due to the low NPE of cattle. Thus, there has been a growing movement worldwide to promote the consumption of non-meat and non-dairy foods so that less energy is wasted feeding animals for the meat industry.

Modeling Ecosystems Energy Flow: Ecological Pyramids

The structure of ecosystems can be visualized with ecological pyramids, which were first described by the pioneering studies of Charles Elton in the 1920s. **Ecological pyramids** show the relative amounts of various parameters (such as number of organisms, energy, and biomass) across trophic levels.

Pyramids of numbers can be either upright or inverted, depending on the ecosystem. As shown in [link], typical grassland during the summer has a base of many plants and the numbers of organisms decrease at each trophic level. However, during the summer in a temperate forest, the base of the pyramid consists of few trees compared with the number of primary consumers, mostly insects. Because trees are large, they have great photosynthetic capability, and dominate other plants in this ecosystem to obtain sunlight. Even in smaller numbers, primary producers in forests are still capable of supporting other trophic levels.

Another way to visualize ecosystem structure is with pyramids of biomass. This pyramid measures the amount of energy converted into living tissue at the different trophic levels. Using the Silver Springs ecosystem example, this data exhibits an upright biomass pyramid ([link]), whereas the pyramid from the English Channel example is inverted. The plants (primary producers) of the Silver Springs ecosystem make up a large percentage of the biomass found there. However, the phytoplankton in the English Channel example make up less biomass than the primary consumers, the zooplankton. As with inverted pyramids of numbers, this inverted pyramid is not due to a lack of productivity from the primary producers, but results from the high turnover rate of the phytoplankton. The phytoplankton are consumed rapidly by the primary consumers, thus, minimizing their biomass at any particular point in time. However, phytoplankton reproduce quickly, thus they are able to support the rest of the ecosystem.

Pyramid ecosystem modeling can also be used to show energy flow through the trophic levels. Notice that these numbers are the same as those used in the energy flow compartment diagram in [link]. Pyramids of energy are always upright, and an ecosystem without sufficient primary productivity cannot be supported. All types of ecological pyramids are useful for characterizing ecosystem structure. However, in the study of energy flow through the ecosystem, pyramids of energy are the most consistent and representative models of ecosystem structure ([link]).

Note:
Art Connection

A. Biomass (dry mass, g/m²)

Silver Springs, Florida

Fishes 5
Fishes 11
Herbivorous insects, snails 37
Decomposers (fungi, bacteria) 5
Plants 809

English Channel

21 Zooplankton
4 Phytoplankton

B. Number of individuals per 0.1 hectare

Grassland (summer)

1 Bird
90,000 Predatory insects
200,000 Herbivorous insects
1,500,000 Grass plants

Temperate forest (summer)

5 Birds
120,000 Predatory insects
150,000 Herbivorous insects
200 trees

C. Energy (kcal/m²/yr)

Silver Springs, Florida

Fishes 21
Fishes 383
Insects, snails 3368
Decomposers (fungi, bacteria) 5060
Plants 20,810

Tertiary (apex) consumer
Secondary consumer
Primary consumer
Primary producer

Ecological pyramids depict the (a) biomass, (b) number of organisms, and (c) energy in each trophic level.

Pyramids depicting the number of organisms or biomass may be inverted, upright, or even diamond-shaped. Energy pyramids, however, are always upright. Why?

Consequences of Food Webs: Biological Magnification

One of the most important environmental consequences of ecosystem dynamics is biomagnification. **Biomagnification** is the increasing concentration of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers. Many substances have been shown to bioaccumulate, including classical studies with the pesticide **d**ichloro**d**iphenyl**t**richloroethane (DDT), which was published in the 1960s bestseller, *Silent Spring*, by Rachel Carson. DDT was a

commonly used pesticide before its dangers became known. In some aquatic ecosystems, organisms from each trophic level consumed many organisms of the lower level, which caused DDT to increase in birds (apex consumers) that ate fish. Thus, the birds accumulated sufficient amounts of DDT to cause fragility in their eggshells. This effect increased egg breakage during nesting and was shown to have adverse effects on these bird populations. The use of DDT was banned in the United States in the 1970s.

Other substances that biomagnify are polychlorinated biphenyls (PCBs), which were used in coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances were best studied in aquatic ecosystems, where fish species at different trophic levels accumulate toxic substances brought through the ecosystem by the primary producers. As illustrated in a study performed by the National Oceanic and Atmospheric Administration (NOAA) in the Saginaw Bay of Lake Huron ([link]), PCB concentrations increased from the ecosystem's primary producers (phytoplankton) through the different trophic levels of fish species. The apex consumer (walleye) has more than four times the amount of PCBs compared to phytoplankton. Also, based on results from other studies, birds that eat these fish may have PCB levels at least one order of magnitude higher than those found in the lake fish.
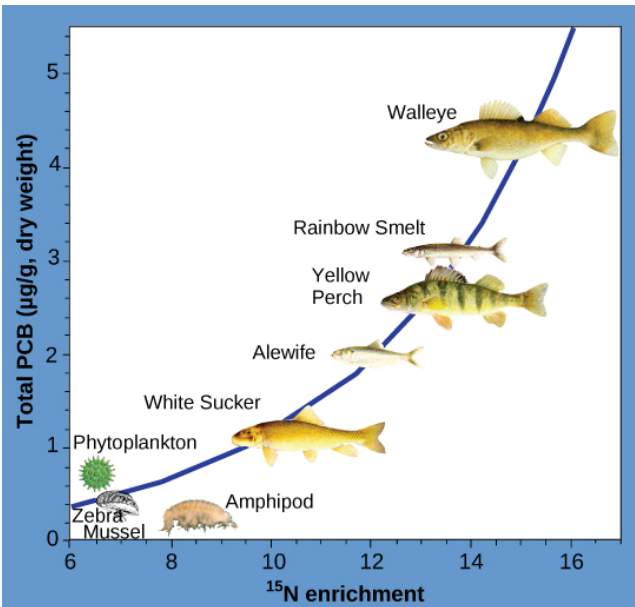
This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Numbers on the x-axis reflect enrichment with heavy isotopes of nitrogen (^{15}N), which is a marker for increasing trophic level. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels. (credit: Patricia Van Hoof, NOAA, GLERL)

Other concerns have been raised by the accumulation of heavy metals, such as mercury and cadmium, in certain types of seafood. The United States Environmental Protection Agency (EPA) recommends that pregnant women and young children should not consume any swordfish, shark, king mackerel, or tilefish because of their high mercury content. These individuals are advised to eat fish low in mercury: salmon, tilapia, shrimp,

pollock, and catfish. Biomagnification is a good example of how ecosystem dynamics can affect our everyday lives, even influencing the food we eat.

Section Summary

Organisms in an ecosystem acquire energy in a variety of ways, which is transferred between trophic levels as the energy flows from the bottom to the top of the food web, with energy being lost at each transfer. The efficiency of these transfers is important for understanding the different behaviors and eating habits of warm-blooded versus cold-blooded animals. Modeling of ecosystem energy is best done with ecological pyramids of energy, although other ecological pyramids provide other vital information about ecosystem structure.

Art Connections

Exercise:

Problem:

[link] Pyramids depicting the number of organisms or biomass may be inverted, upright, or even diamond-shaped. Energy pyramids, however, are always upright. Why?

Solution:

[link] Pyramids of organisms may be inverted or diamond-shaped because a large organism, such as a tree, can sustain many smaller organisms. Likewise, a low biomass of organisms can sustain a larger biomass at the next trophic level because the organisms reproduce rapidly and thus supply continuous nourishment. Energy pyramids, however, must always be upright because of the laws of thermodynamics. The first law of thermodynamics states that energy can neither be created nor destroyed; thus, each trophic level must acquire energy from the trophic level below. The second law of thermodynamics states that, during the transfer of energy, some energy

is always lost as heat; thus, less energy is available at each higher trophic level.

Review Questions

Exercise:

Problem:

The weight of living organisms in an ecosystem at a particular point in time is called:

   a. energy
   b. production
   c. entropy
   d. biomass

Solution:

D

Exercise:

Problem:

Which term describes the process whereby toxic substances increase along trophic levels of an ecosystem?

   a. biomassification
   b. biomagnification
   c. bioentropy
   d. heterotrophy

Solution:

B

Exercise:

Problem:

Organisms that can make their own food using inorganic molecules are called:

   a. autotrophs
   b. heterotrophs
   c. photoautotrophs
   d. chemoautotrophs

Solution:

   D

Exercise:

Problem:

In the English Channel ecosystem, the number of primary producers is smaller than the number of primary consumers because_____.

   a. the apex consumers have a low turnover rate
   b. the primary producers have a low turnover rate
   c. the primary producers have a high turnover rate
   d. the primary consumers have a high turnover rate

Solution:

   C

Exercise:

Problem:

What law of chemistry determines how much energy can be transferred when it is converted from one form to another?

   a. the first law of thermodynamics

b. the second law of thermodynamics
c. the conservation of matter
d. the conservation of energy

Solution:

B

Free Response

Exercise:

Problem:

Compare the three types of ecological pyramids and how well they describe ecosystem structure. Identify which ones can be inverted and give an example of an inverted pyramid for each.

Solution:

Pyramids of numbers display the number of individual organisms on each trophic level. These pyramids can be either upright or inverted, depending on the number of the organisms. Pyramids of biomass display the weight of organisms at each level. Inverted pyramids of biomass can occur when the primary producer has a high turnover rate. Pyramids of energy are usually upright and are the best representation of energy flow and ecosystem structure.

Exercise:

Problem:

How does the amount of food a warm blooded-animal (endotherm) eats relate to its net production efficiency (NPE)?

Solution:

NPE measures the rate at which one trophic level can use and make biomass from what it attained in the previous level, taking into account respiration, defecation, and heat loss. Endotherms have high metabolism and generate a lot of body heat. Although this gives them advantages in their activity level in colder temperatures, these organisms are 10 times less efficient at harnessing the energy from the food they eat compared with cold-blooded animals, and thus have to eat more and more often.

Glossary

assimilation
    biomass consumed and assimilated from the previous trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste

biomagnification
    increasing concentrations of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers

biomass
    total weight, at the time of measurement, of living or previously living organisms in a unit area within a trophic level

chemoautotroph
    organism capable of synthesizing its own food using energy from inorganic molecules

ecological pyramid
    (also, Eltonian pyramid) graphical representation of different trophic levels in an ecosystem based of organism numbers, biomass, or energy content

gross primary productivity
    rate at which photosynthetic primary producers incorporate energy from the sun

net consumer productivity
    energy content available to the organisms of the next trophic level

net primary productivity
    energy that remains in the primary producers after accounting for the
    organisms' respiration and heat loss

net production efficiency (NPE)
    measure of the ability of a trophic level to convert the energy it
    receives from the previous trophic level into biomass

trophic level transfer efficiency (TLTE)
    energy transfer efficiency between two successive trophic levels

Biogeochemical Cycles
By the end of this section, you will be able to:

- Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur
- Explain how human activities have impacted these cycles and the potential consequences for Earth

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules—carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur—take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the Earth's surface. Geologic processes, such as weathering, erosion, water drainage, and the subduction of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a **biogeochemical cycle**.

Water contains hydrogen and oxygen, which is essential to all living processes. The **hydrosphere** is the area of the Earth where water movement and storage occurs: as liquid water on the surface and beneath the surface or frozen (rivers, lakes, oceans, groundwater, polar ice caps, and glaciers), and as water vapor in the atmosphere. Carbon is found in all organic macromolecules and is an important constituent of fossil fuels. Nitrogen is a major component of our nucleic acids and proteins and is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur, critical to the 3–D folding of proteins (as in disulfide binding), is released into the atmosphere by the burning of fossil fuels, such as coal.

The cycling of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or

slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

The Water (Hydrologic) Cycle

Water is the basis of all living processes. The human body is more than 1/2 water and human cells are more than 70 percent water. Thus, most land animals need a supply of fresh water to survive. However, when examining the stores of water on Earth, 97.5 percent of it is non-potable salt water ([link]). Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1 percent of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on the small amount of fresh surface water supply, a lack of which can have massive effects on ecosystem dynamics. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean. Although this pursuit of drinkable water has been ongoing throughout human history, the supply of fresh water is still a major issue in modern times.
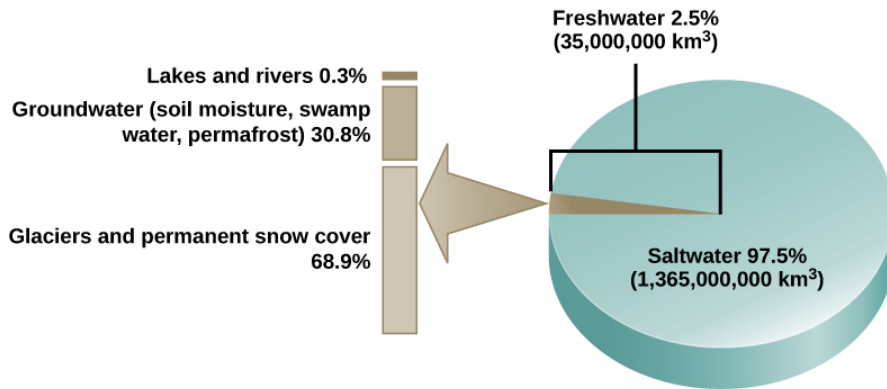
Only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things.

Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems, some located on distant parts of the Earth. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. [link] illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. **Residence time** is a measure of the average time an individual water molecule stays in a particular reservoir. A large amount of the Earth's water is locked in place in these reservoirs as ice, beneath the ground, and in the ocean, and, thus, is unavailable for short-term cycling (only surface water can evaporate).

Average Residence Time for Water Molecules

Biospheric (in living organisms) 1 week

Atmospheric 1.5 weeks

Rivers 2 weeks

Soil moisture 2 weeks–1 year

Swamps 1–10 years

Lakes & reservoirs 10 years

Oceans & seas 4,000 years

Groundwater 2 weeks to 10,000 years

Glaciers and permafrost 1,000–10,000 years

This graph shows the average residence time for water molecules in the Earth's water reservoirs.

There are various processes that occur during the cycling of water, shown in [link]. These processes include the following:

- evaporation/sublimation
- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

The water cycle is driven by the sun's energy as it warms the oceans and other surface waters. This leads to the evaporation (water to water vapor) of liquid surface water and the sublimation (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets and is eventually followed by precipitation (rain or snow), which returns water to the Earth's surface. Rain eventually permeates into the ground, where it may evaporate again if it is near the surface, flow beneath

the surface, or be stored for long periods. More easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. The environmental effects of runoff will be discussed later as these cycles are described.
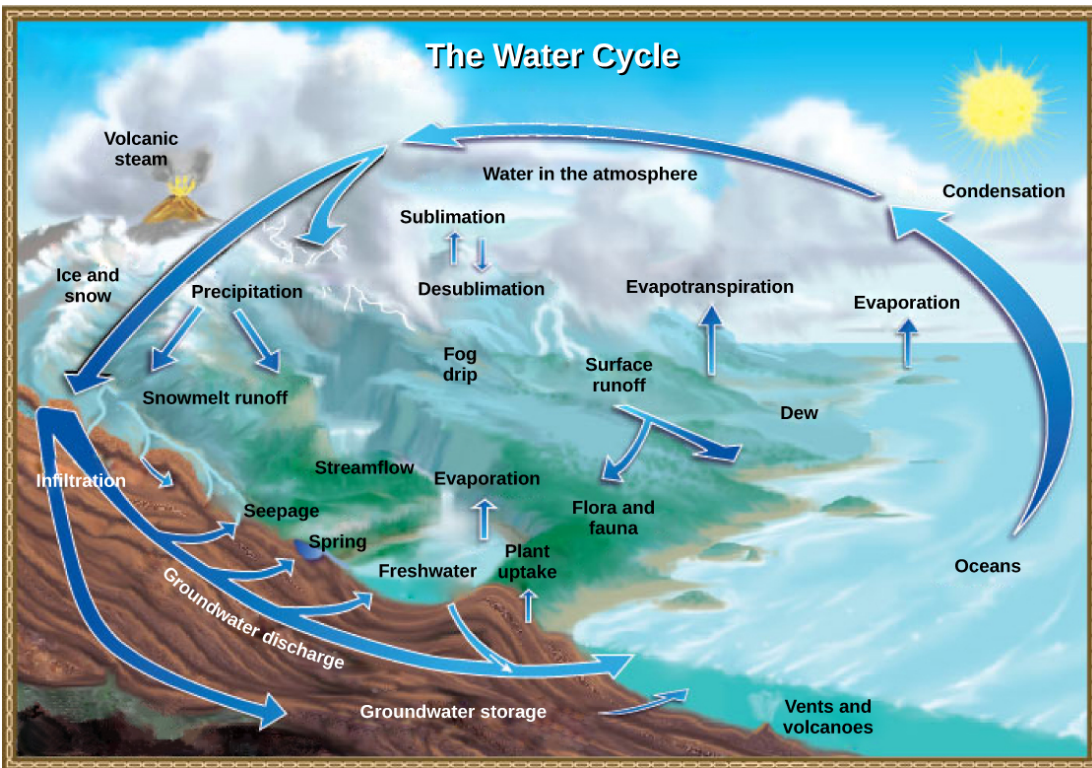
Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Carbon Cycle

Carbon is the second most abundant element in living organisms. Carbon is present in all organic molecules, and its role in the structure of macromolecules is of primary importance to living organisms. Carbon compounds contain especially high energy, particularly those derived from fossilized organisms, mainly plants, which humans use as fuel. Since the 1800s, the number of countries using massive amounts of fossil fuels has increased. Since the beginning of the Industrial Revolution, global demand for the Earth's limited fossil fuel supplies has risen; therefore, the amount of

carbon dioxide in our atmosphere has increased. This increase in carbon dioxide has been associated with climate change and other disturbances of the Earth's ecosystems and is a major environmental concern worldwide. Thus, the "carbon footprint" is based on how much carbon dioxide is produced and how much fossil fuel countries consume.

The carbon cycle is most easily studied as two interconnected sub-cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes. The entire carbon cycle is shown in [link].
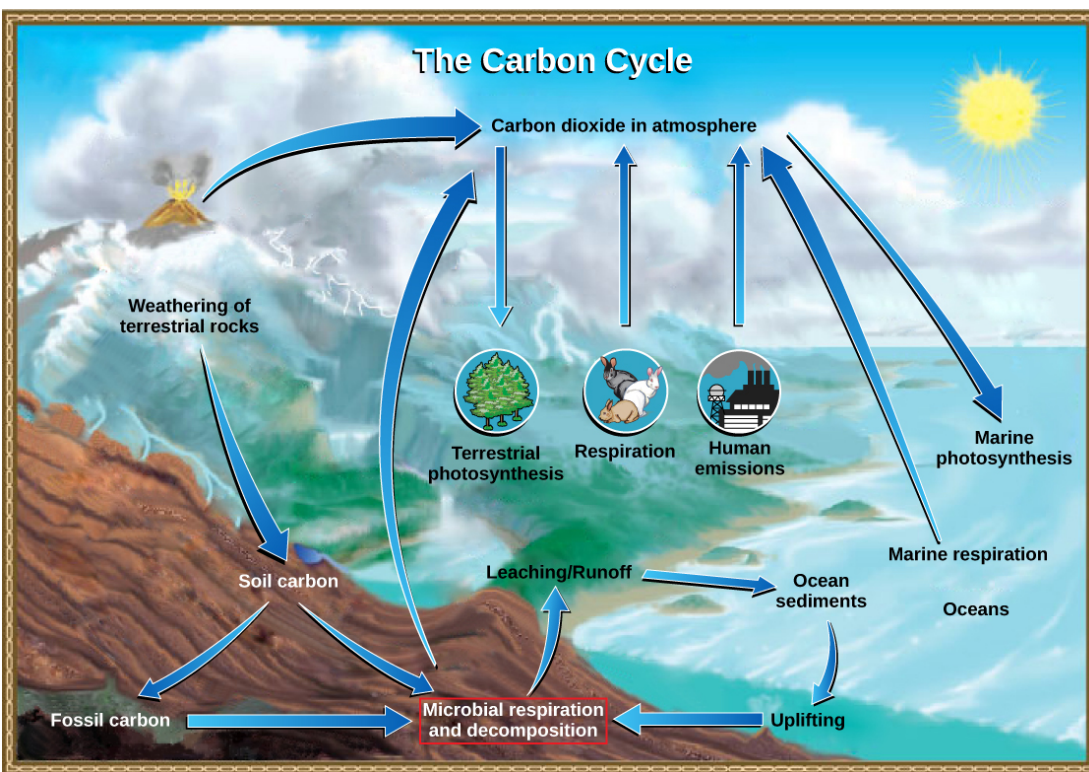
Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions, bring this stored carbon back

into the carbon cycle. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Biological Carbon Cycle

Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs within and between ecosystems by way of atmospheric carbon dioxide. Carbon dioxide is the basic building block that most autotrophs use to build multi-carbon, high energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds thereby store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (carbonic acid, $H_2CO_3^-$). However carbon dioxide is acquired, a by-product of the process is oxygen. The photosynthetic organisms are responsible for depositing approximately 21 percent oxygen content of the atmosphere that we observe today.

Heterotrophs and autotrophs are partners in biological carbon exchange (especially the primary consumers, largely herbivores). Heterotrophs acquire the high-energy carbon compounds from the autotrophs by consuming them, and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Gas exchange through the atmosphere and water is one way that the carbon cycle connects all living organisms on Earth.

The Biogeochemical Carbon Cycle

The movement of carbon through the land, water, and air is complex, and in many cases, it occurs much more slowly geologically than as seen between living organisms. Carbon is stored for long periods in what are known as carbon reservoirs, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, land sediments (including fossil fuels), and the Earth's interior.

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide and is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each location, and each one affects the other reciprocally. Carbon dioxide (CO_2) from the atmosphere dissolves in water and combines with water molecules to form carbonic acid, and then it ionizes to carbonate and bicarbonate ions ([link])

Step 1: CO_2 (atmospheric) $\rightleftharpoons$ CO_2 (dissolved)
Step 2: CO_2 (dissolved) + H_2O $\rightleftharpoons$ H_2CO_3 (carbonic acid)
Step 3: H_2CO_3 $\rightleftharpoons$ + H^+ + HCO_3^- (biocarbonate ion)
Step 4: HCO_3^- $\rightleftharpoons$ H^+ + CO_3^{2-} (carbonate ion)

Carbon dioxide reacts with water to form bicarbonate and carbonate ions.

The equilibrium coefficients are such that more than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate ($CaCO_3$), a major component of marine organism shells. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

On land, carbon is stored in soil as a result of the decomposition of living organisms (by decomposers) or from weathering of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Deeper underground, on land and at sea, are fossil fuels: the anaerobically decomposed remains of plants that take millions of years to form. Fossil fuels are considered a non-renewable resource because their use far exceeds their rate of formation. A **non-renewable resource**, such as fossil fuel, is either regenerated very slowly or not at all. Another way for carbon to enter the atmosphere is from land (including land beneath the surface of the ocean) by the eruption of volcanoes and other geothermal systems. Carbon sediments from the ocean floor are taken deep within the Earth by the process of **subduction**: the movement of one tectonic plate beneath another. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.

Carbon dioxide is also added to the atmosphere by the animal husbandry practices of humans. The large numbers of land animals raised to feed the Earth's growing population results in increased carbon dioxide levels in the atmosphere due to farming practices and the respiration and methane production. This is another example of how human activity indirectly affects biogeochemical cycles in a significant way. Although much of the debate about the future effects of increasing atmospheric carbon on climate change focuses on fossils fuels, scientists take natural processes, such as

volcanoes and respiration, into account as they model and predict the future impact of this increase.

The Nitrogen Cycle

Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly bonded, triple covalent N_2) even though this molecule comprises approximately 78 percent of the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through nitrogen fixation (conversion of N_2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to "fix" nitrogen. *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. As shown in [link], the nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the ammonification process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by nitrifying bacteria, such as *Nitrosomonas*, through nitrification. Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of denitrification occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to re-enter the atmosphere.

Note:

Art Connection

The Nitrogen Cycle
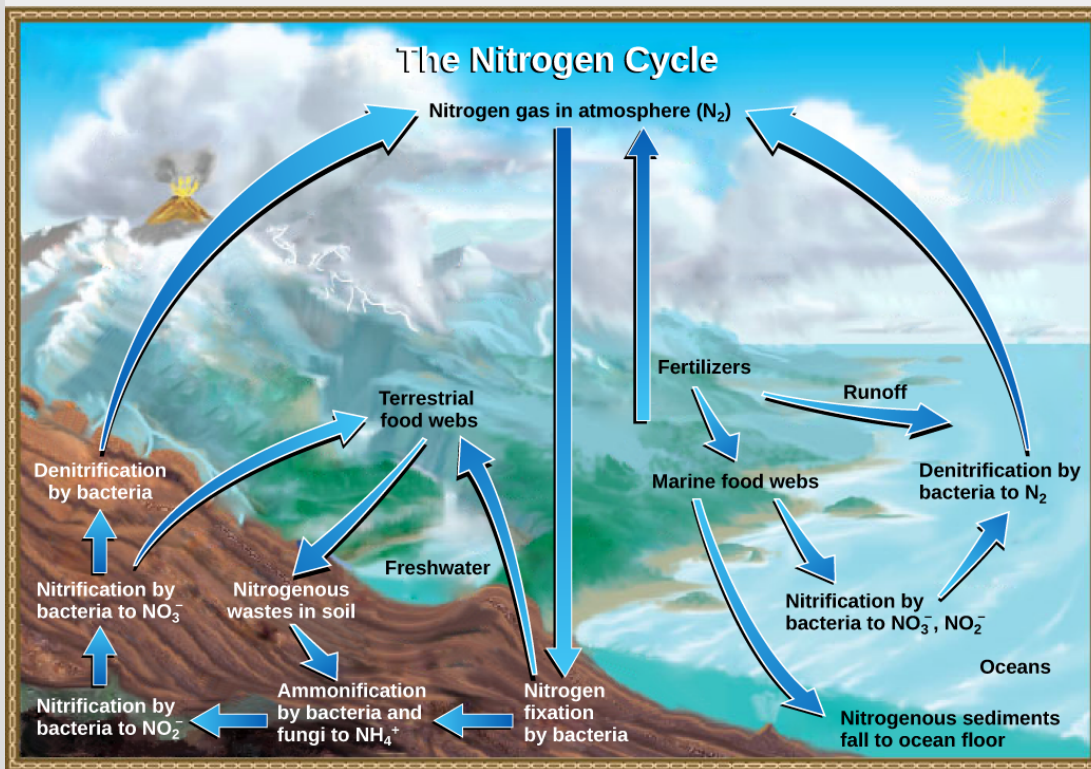
Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Which of the following statements about the nitrogen cycle is false?

a. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
b. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
c. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
d. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers in agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on Earth's ecosystems including the production of acid rain (as nitric acid, HNO_3) and greenhouse gas (as nitrous oxide, N_2O) potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater **eutrophication**, a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the Earth's surface and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle. [footnote]

Scott L. Morford, Benjamin Z. Houlton, and Randy A. Dahlgren, "Increased Forest Ecosystem Carbon and Nitrogen Storage from Nitrogen Rich Bedrock," *Nature* 477, no. 7362 (2011): 78–81.

The Phosphorus Cycle

Phosphorus is an essential nutrient for living processes; it is a major component of nucleic acid and phospholipids, and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems ([link]).

Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily

from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is moved to land over geologic time by the uplifting of areas of the Earth's surface.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.
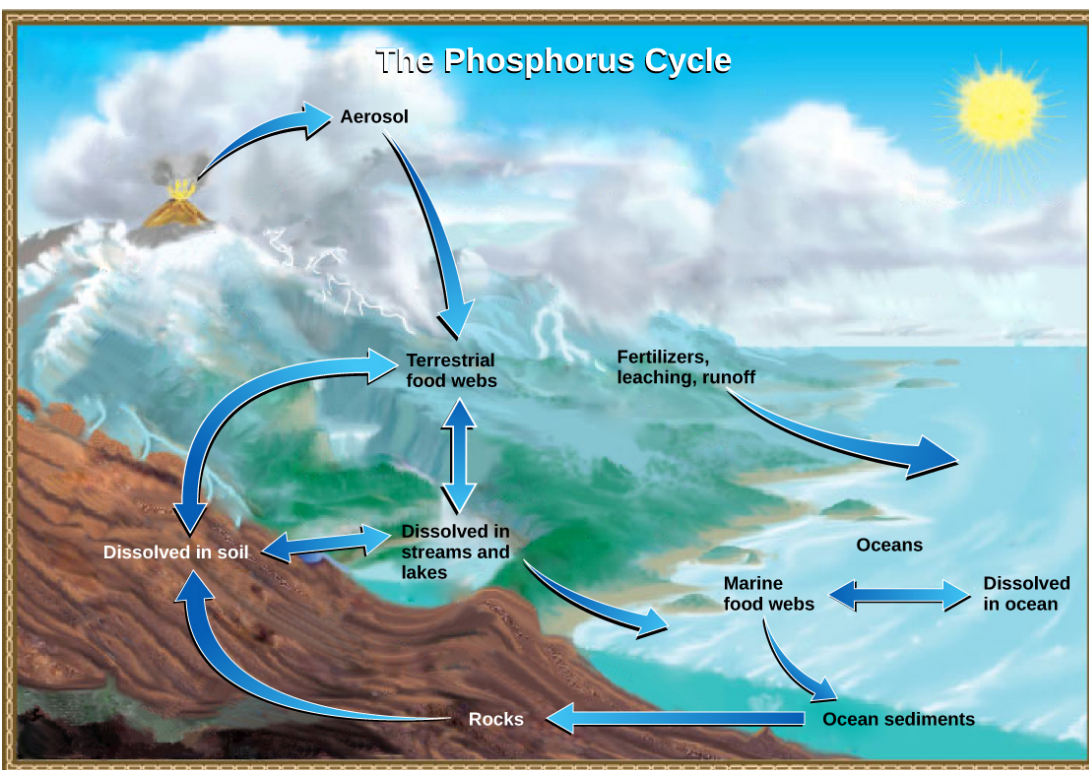
In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it

forms sediment. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers ([link]).
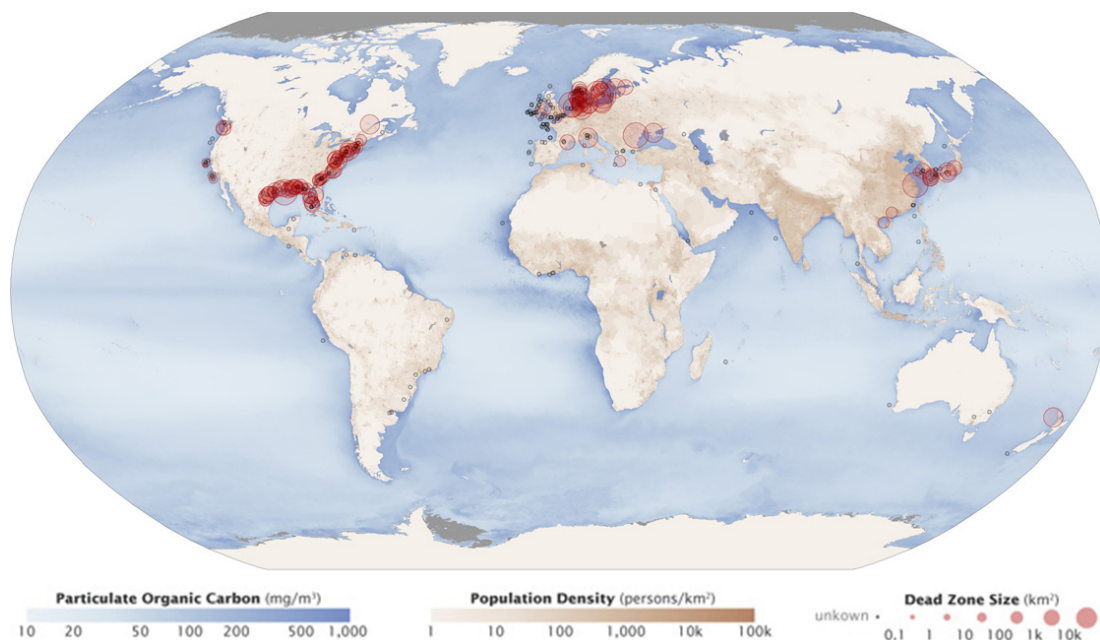
Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

A **dead zone** is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years, and more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 8463 square miles. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States.

Note:
Everyday Connection
Chesapeake Bay

(a)

(b)

This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in

the bay. (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army)

The Chesapeake Bay has long been valued as one of the most scenic areas on Earth; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms. Several species have declined in the Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overharvesting. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by non-profit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for inter-state cooperation to gain successful restoration.

The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

The Sulfur Cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns, and hence their functions. As shown in [link], sulfur cycles between the oceans, land, and atmosphere. Atmospheric sulfur is found in the form of sulfur dioxide (SO_2) and enters the atmosphere in three ways: from the decomposition of organic molecules, from volcanic activity and geothermal vents, and from the burning of fossil fuels by humans.
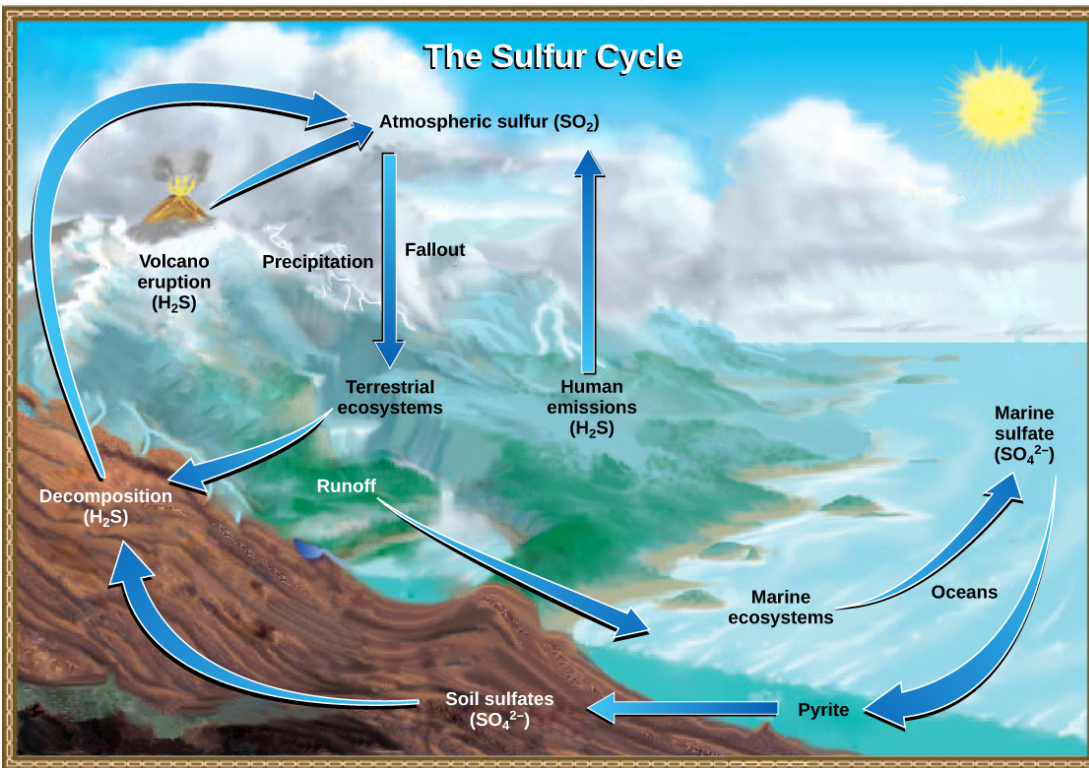
Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the Earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil and atmosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and geothermal vents ([link]). Atmospheric sulfur is found in the form of sulfur dioxide (SO_2), and as rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfuric acid (H_2SO_4). Sulfur can also fall directly from the atmosphere in a process called **fallout**. Also, the weathering of sulfur-containing rocks releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplifting of ocean sediments.

Terrestrial ecosystems can then make use of these soil sulfates (SO_{4-}), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide (H_2S) gas.

At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems ([link]) rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially from coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. As rain falls through this gas, it creates the phenomenon known as acid rain. **Acid rain** is corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid,

which causes damage to aquatic ecosystems. Acid rain damages the natural environment by lowering the pH of lakes, which kills many of the resident fauna; it also affects the man-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years. These examples show the wide-ranging effects of human activities on our environment and the challenges that remain for our future.

Note:
Link to Learning

Click this link to learn more about global climate change.

Section Summary

Mineral nutrients are cycled through ecosystems and their environment. Of particular importance are water, carbon, nitrogen, phosphorus, and sulfur. All of these cycles have major impacts on ecosystem structure and function. As human activities have caused major disturbances to these cycles, their study and modeling is especially important. A variety of human activities, such as pollution, oil spills, and events) have damaged ecosystems, potentially causing global climate change. The health of Earth depends on understanding these cycles and how to protect the environment from irreversible damage.

Art Connections

Exercise:

Problem:

[link] Which of the following statements about the nitrogen cycle is false?

    a. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
    b. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
    c. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
    d. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

Solution:

[link] C: Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).

Review Questions

Exercise:

Problem:

The movement of mineral nutrients through organisms and their environment is called a _____ cycle.

    a. biological
    b. bioaccumulation
    c. biogeochemical
    d. biochemical

Solution:

C

Exercise:

Problem: Carbon is present in the atmosphere as _____.

    a. carbon dioxide
    b. carbonate ion
    c. carbon dust
    d. carbon monoxide

Solution:

A

Exercise:

Problem: The majority of water found on Earth is:

    a. ice
    b. water vapor
    c. fresh water
    d. salt water

Solution:

D

Exercise:

Problem:

The average time a molecule spends in its reservoir is known as _____.

    a. residence time
    b. restriction time
    c. resilience time

d. storage time

Solution:

A

Exercise:

Problem:

The process whereby oxygen is depleted by the growth of microorganisms due to excess nutrients in aquatic systems is called _____.

   a. dead zoning
   b. eutrophication
   c. retrofication
   d. depletion

Solution:

B

Exercise:

Problem:

The process whereby nitrogen is brought into organic molecules is called _____.

   a. nitrification
   b. denitrification
   c. nitrogen fixation
   d. nitrogen cycling

Solution:

C

Free Response

Exercise:

Problem:

Describe nitrogen fixation and why it is important to agriculture.

Solution:

Nitrogen fixation is the process of bringing nitrogen gas from the atmosphere and incorporating it into organic molecules. Most plants do not have this capability and must rely on free-living or symbiotic bacteria to do this. As nitrogen is often the limiting nutrient in the growth of crops, farmers make use of artificial fertilizers to provide a nitrogen source to the plants as they grow.

Exercise:

Problem:

What are the factors that cause dead zones? Describe eutrophication, in particular, as a cause.

Solution:

Many factors can kill life in a lake or ocean, such as eutrophication by nutrient-rich surface runoff, oil spills, toxic waste spills, changes in climate, and the dumping of garbage into the ocean. Eutrophication is a result of nutrient-rich runoff from land using artificial fertilizers high in nitrogen and phosphorus. These nutrients cause the rapid and excessive growth of microorganisms, which deplete local dissolved oxygen and kill many fish and other aquatic organisms.

Exercise:

Problem:

Why are drinking water supplies still a major concern for many countries?

Solution:

Most of the water on Earth is salt water, which humans cannot drink unless the salt is removed. Some fresh water is locked in glaciers and polar ice caps, or is present in the atmosphere. The Earth's water supplies are threatened by pollution and exhaustion. The effort to supply fresh drinking water to the planet's ever-expanding human population is seen as a major challenge in this century.

Glossary

acid rain
   corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid; can damage structures and ecosystems

biogeochemical cycle
   cycling of mineral nutrients through ecosystems and through the non-living world

dead zone
   area within an ecosystem in lakes and near the mouths of rivers where large areas of ecosystems are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities

eutrophication
   process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna

fallout

direct deposit of solid minerals on land or in the ocean from the atmosphere

hydrosphere
area of the Earth where water movement and storage occurs

non-renewable resource
resource, such as fossil fuel, that is either regenerated very slowly or not at all

residence time
measure of the average time an individual water molecule stays in a particular reservoir

subduction
movement of one tectonic plate beneath another

Introduction
class="introduction"

Lake Victoria in Africa, shown in this satellite image, was the site of one of the most extraordinary evolutionary findings on the planet, as well as a casualty of devastating biodiversity loss. (credit: modification of work by Rishabh Tatiraju, using NASA World Wind software)
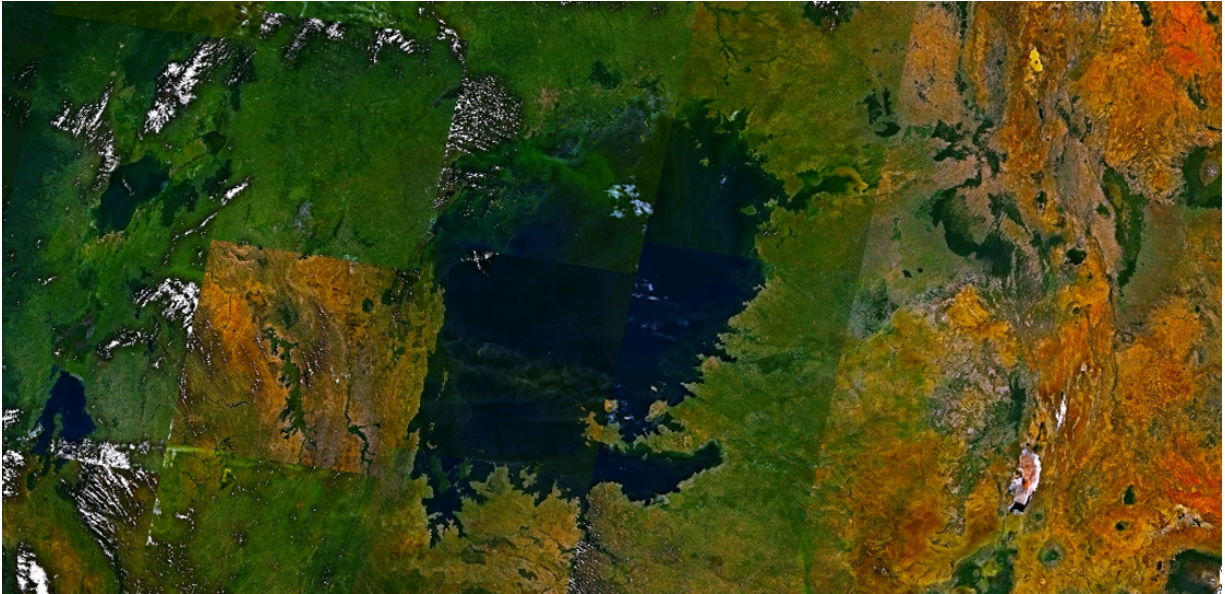
In the 1980s, biologists working in Lake Victoria in Africa discovered one of the most extraordinary products of evolution on the planet. Located in the Great Rift Valley, Lake Victoria is a large lake about 68,900 km^2 in area (larger than Lake Huron, the second largest of North America's Great Lakes). Biologists were studying species of a family of fish called cichlids. They found that as they sampled for fish in different locations of the lake, they never stopped finding new species, and they identified nearly 500 evolved types of cichlids. But while studying these variations, they quickly discovered that the invasive Nile Perch was destroying the lake's cichlid population, bringing hundreds of cichlid species to extinction with devastating rapidity.

The Biodiversity Crisis
By the end of this section, you will be able to:

- Define biodiversity
- Describe biodiversity as the equilibrium of naturally fluctuating rates of extinction and speciation
- Identify historical causes of high extinction rates in Earth's history

Traditionally, ecologists have measured **biodiversity**, a general term for the variety present in the biosphere, by taking into account both the number of species and their commonness. Biodiversity can be estimated at a number of levels of organization of living things. These estimation indexes, which came from information theory, are most useful as a first step in quantifying biodiversity between and within ecosystems; they are less useful when the main concern among conservation biologists is simply the loss of biodiversity. However, biologists recognize that measures of biodiversity, in terms of species diversity, may help focus efforts to preserve the biologically or technologically important elements of biodiversity.

The Lake Victoria cichlids provide an example through which we can begin to understand biodiversity. The biologists studying cichlids in the 1980s discovered hundreds of cichlid species representing a variety of specializations to particular habitat types and specific feeding strategies: eating plankton floating in the water, scraping and then eating algae from rocks, eating insect larvae from the bottom, and eating the eggs of other species of cichlid. The cichlids of Lake Victoria are the product of an **adaptive radiation**. An adaptive radiation is a rapid (less than three million years in the case of the Lake Victoria cichlids) branching through speciation of a phylogenetic tree into many closely related species; typically, the species "radiate" into different habitats and niches. The Galápagos finches are an example of a modest adaptive radiation with 15 species. The cichlids of Lake Victoria are an example of a spectacular adaptive radiation that includes about 500 species.

At the time biologists were making this discovery, some species began to quickly disappear. A culprit in these declines was a species of large fish that was introduced to Lake Victoria by fisheries to feed the people living around the lake. The Nile perch was introduced in 1963, but lay low until the 1980s when its populations began to surge. The Nile perch population grew by consuming cichlids, driving species after species to the point of **extinction** (the disappearance of a species). In fact, there were several factors that played a role in the extinction of perhaps 200 cichlid species in Lake Victoria: the Nile perch, declining lake water quality due to agriculture and land clearing on the shores of Lake Victoria, and increased fishing pressure. Scientists had not even catalogued all of the species present—so many were lost that were never named. The diversity is now a shadow of what it once was.

The cichlids of Lake Victoria are a thumbnail sketch of contemporary rapid species loss that occurs all over Earth and is caused by human activity. Extinction is a natural process of macroevolution that occurs at the rate of about one out of 1 million species becoming extinct per year. The fossil record reveals that there have been five periods of mass extinction in history with much higher rates of species loss, and the rate of species loss today is comparable to those periods of mass extinction. However, there is a major difference between the previous mass extinctions and the current extinction we are experiencing: human activity. Specifically, three human activities have a major impact: destruction of habitat, introduction of exotic species, and over-harvesting. Predictions of species loss within the next century, a tiny amount of time on geological timescales, range from 10 percent to 50 percent. Extinctions on this scale have only happened five other times in the history of the planet, and they have been caused by cataclysmic events that changed the course of the history of life in each instance. Earth is now in one of those times.

Types of Biodiversity

Scientists generally accept that the term biodiversity describes the number and kinds of species in a location or on the planet. Species can be difficult to define, but most biologists still feel comfortable with the concept and are able to identify and count eukaryotic species in most contexts. Biologists have also identified alternate measures of biodiversity, some of which are important for planning how to preserve biodiversity.

Genetic diversity is one of those alternate concepts. Genetic diversity or variation is the raw material for adaptation in a species. A species' future potential for adaptation depends on the genetic diversity held in the

genomes of the individuals in populations that make up the species. The same is true for higher taxonomic categories. A genus with very different types of species will have more genetic diversity than a genus with species that look alike and have similar ecologies. If there were a choice between one of these genera of species being preserved, the one with the greatest potential for subsequent evolution is the most genetically diverse one. It would be ideal not to have to make such choices, but increasingly this may be the norm.

Many genes code for proteins, which in turn carry out the metabolic processes that keep organisms alive and reproducing. Genetic diversity can be measured as **chemical diversity** in that different species produce a variety of chemicals in their cells, both the proteins as well as the products and byproducts of metabolism. This chemical diversity has potential benefit for humans as a source of pharmaceuticals, so it provides one way to measure diversity that is important to human health and welfare.

Humans have generated diversity in domestic animals, plants, and fungi. This diversity is also suffering losses because of migration, market forces, and increasing globalism in agriculture, especially in heavily populated regions such as China, India, and Japan. The human population directly depends on this diversity as a stable food source, and its decline is troubling biologists and agricultural scientists.

It is also useful to define **ecosystem diversity**, meaning the number of different ecosystems on the planet or in a given geographic area ([link]). Whole ecosystems can disappear even if some of the species might survive by adapting to other ecosystems. The loss of an ecosystem means the loss of interactions between species, the loss of unique features of coadaptation, and the loss of biological productivity that an ecosystem is able to create. An example of a largely extinct ecosystem in North America is the prairie ecosystem. Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. They are now all but gone, replaced by crop fields, pasture lands, and suburban sprawl. Many of the species survive, but the hugely productive ecosystem that was responsible for creating the most productive agricultural soils is now gone. As a consequence, soils are disappearing or must be maintained at greater expense.

(a)

(b)

The variety of ecosystems on Earth—from (a) coral reef to (b) prairie—enables a great diversity of species to exist. (credit a: modification of work by Jim

Current Species Diversity

Despite considerable effort, knowledge of the species that inhabit the planet is limited. A recent estimate suggests that the eukaryote species for which science has names, about 1.5 million species, account for less than 20 percent of the total number of eukaryote species present on the planet (8.7 million species, by one estimate). Estimates of numbers of prokaryotic species are largely guesses, but biologists agree that science has only begun to catalog their diversity. Even with what is known, there is no central repository of names or samples of the described species; therefore, there is no way to be sure that the 1.5 million descriptions is an accurate number. It is a best guess based on the opinions of experts in different taxonomic groups. Given that Earth is losing species at an accelerating pace, science is very much in the place it was with the Lake Victoria cichlids: knowing little about what is being lost. [link] presents recent estimates of biodiversity in different groups.

Estimates of the Numbers of Described and Predicted Species by Taxonomic Group				
	Mora et al. 2011[footnote] **Mora Camilo et al., "How Many Species Are There on Earth and in the Ocean?"** *PLoS Biology* **(2011), doi:10.1371/journal.pbio.1001127.**		**Chapman 2009**[footnote] **Arthur D. Chapman,** *Numbers of Living Species in* **2nd ed. (Canberra, AU: Australian Biological Reso http://www.environment.gov.au/biodiversity/abrs/p numbers/2009/pubs/nlsaw-2nd-complete.pdf.**	
	Described	Predicted	Described	Predicted
Animalia	1,124,516	9,920,000	1,424,153	6,836,330
Chromista	17,892	34,900	25,044	200,500
Fungi	44,368	616,320	98,998	1,500,000
Plantae	224,244	314,600	310,129	390,800
Protozoa	16,236	72,800	28,871	1,000,000
Prokaryotes	—	—	10,307	1,000,000
Total	1,438,769	10,960,000	1,897,502	10,897,630

There are various initiatives to catalog described species in accessible ways, and the internet is facilitating that effort. Nevertheless, it has been pointed out that at the current rate of species description, which according to the

State of Observed Species Report is 17,000 to 20,000 new species per year, it will take close to 500 years to finish describing life on this planet.[footnote] Over time, the task becomes both increasingly impossible and increasingly easier as extinction removes species from the planet.

International Institute for Species Exploration (IISE), *2011 State of Observed Species (SOS)*. Tempe, AZ: IISE, 2011. Accessed May, 20, 2012. http://species.asu.edu/SOS.

Naming and counting species may seem an unimportant pursuit given the other needs of humanity, but it is not simply an accounting. Describing species is a complex process by which biologists determine an organism's unique characteristics and whether or not that organism belongs to any other described species. It allows biologists to find and recognize the species after the initial discovery, and allows them to follow up on questions about its biology. In addition, the unique characteristics of each species make it potentially valuable to humans or other species on which humans depend. Understanding these characteristics is the value of finding and naming species.

Patterns of Biodiversity

Biodiversity is not evenly distributed on Earth. Lake Victoria contained almost 500 species of cichlids alone, ignoring the other fish families present in the lake. All of these species were found only in Lake Victoria; therefore, the 500 species of cichlids were endemic. **Endemic species** are found in only one location. Endemics with highly restricted distributions are particularly vulnerable to extinction. Higher taxonomic levels, such as genera and families, can also be endemic. Lake Huron contains about 79 species of fish, all of which are found in many other lakes in North America. What accounts for the difference in fish diversity in these two lakes? Lake Victoria is a tropical lake, while Lake Huron is a temperate lake. Lake Huron in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old. Biogeographers have suggested these two factors, latitude and age, are two of several hypotheses to explain biodiversity patterns on the planet.

> **Note:**
> Career Connection
> **Biogeographer**
> Biogeography is the study of the distribution of the world's species—both in the past and in the present. The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how environmental changes impact the distribution of a species; it has also been critical to developing evolutionary theory. Biogeographers need to understand both biology and ecology. They also need to be well-versed in evolutionary studies, soil science, and climatology.
> There are three main fields of study under the heading of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. Ecological biogeography studies the current factors affecting the distribution of plants and animals. Historical biogeography, as the name implies, studies the past distribution of species. Conservation biogeography, on the other hand, is focused on the protection and restoration of species based upon known historical and current ecological information. Each of these fields considers both zoogeography and phytogeography—the past and present distribution of animals and plants.

One of the oldest observed patterns in ecology is that species biodiversity in almost every taxonomic group increases as latitude declines. In other words, biodiversity increases closer to the equator ([link]).
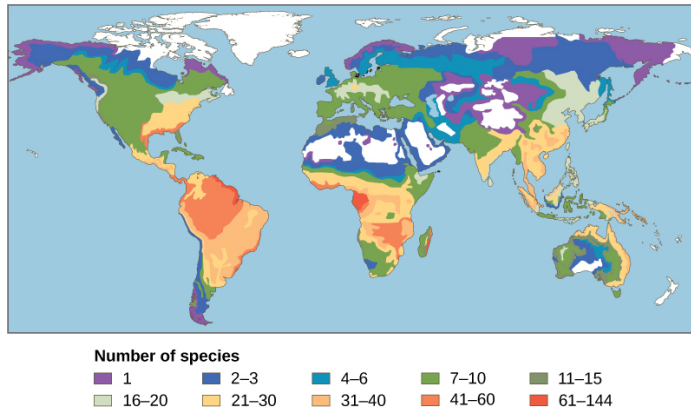
This map illustrates the number of amphibian species across the globe and shows the trend toward higher biodiversity at lower latitudes. A similar pattern is observed for most taxonomic groups.

It is not yet clear why biodiversity increases closer to the equator, but hypotheses include the greater age of the ecosystems in the tropics versus temperate regions that were largely devoid of life or drastically impoverished during the last glaciation. The idea is that greater age provides more time for speciation. Another possible explanation is the increased energy the tropics receive from the sun versus the decreased energy that temperate and polar regions receive. It is not entirely clear how greater energy input could translate into more species. The complexity of tropical ecosystems may promote speciation by increasing the **heterogeneity**, or number of ecological niches, in the tropics relative to higher latitudes. The greater heterogeneity provides more opportunities for coevolution, specialization, and perhaps greater selection pressures leading to population differentiation. However, this hypothesis suffers from some circularity—ecosystems with more species encourage speciation, but how did they get more species to begin with? The tropics have been perceived as being more stable than temperate regions, which have a pronounced climate and day-length seasonality. The tropics have their own forms of seasonality, such as rainfall, but they are generally assumed to be more stable environments and this stability might promote speciation.

Regardless of the mechanisms, it is certainly true that all levels of biodiversity are greatest in the tropics. Additionally, the rate of endemism is highest, and there are more biodiversity hotspots. However, this richness of diversity also means that knowledge of species is lowest, and there is a high potential for biodiversity loss.

Conservation of Biodiversity

In 1988, British environmentalist Norman Myers developed a conservation concept to identify areas rich in species and at significant risk for species loss: biodiversity hotspots. **Biodiversity hotspots** are geographical areas that contain high numbers of endemic species. The purpose of the concept was to identify important locations on the planet for conservation efforts, a kind of conservation triage. By protecting hotspots, governments are able to protect a larger number of species. The original criteria for a hotspot included the presence of 1500 or more endemic plant species and 70 percent of the area disturbed by human activity. There are now 34 biodiversity hotspots ([link]) containing large numbers of endemic species, which include half of Earth's endemic plants.
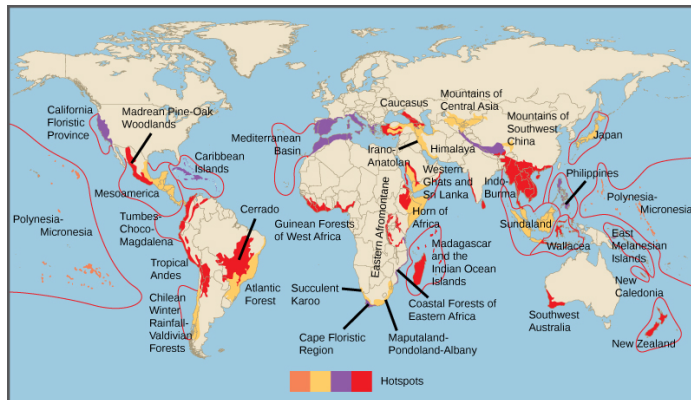
Conservation International has identified 34 biodiversity hotspots, which cover only 2.3 percent of the Earth's surface but have endemic to them 42 percent of the terrestrial vertebrate species and 50 percent of the world's plants.

Biodiversity Change through Geological Time

The number of species on the planet, or in any geographical area, is the result of an equilibrium of two evolutionary processes that are ongoing: speciation and extinction. Both are natural "birth" and "death" processes of macroevolution. When speciation rates begin to outstrip extinction rates, the number of species will increase; likewise, the number of species will decrease when extinction rates begin to overtake speciation rates. Throughout Earth's history, these two processes have fluctuated—sometimes leading to dramatic changes in the number of species on Earth as reflected in the fossil record ([link]).
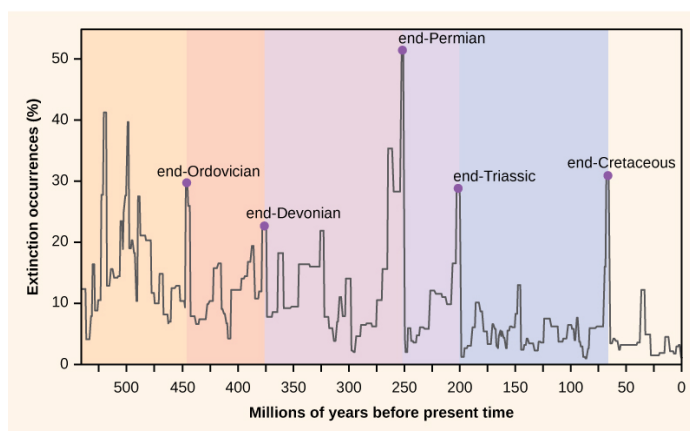
Percent extinction occurrences as reflected in the fossil record have fluctuated throughout Earth's history. Sudden and dramatic losses of biodiversity, called mass extinctions, have occurred five times.

Paleontologists have identified five strata in the fossil record that appear to show sudden and dramatic (greater than half of all extant species disappearing from the fossil record) losses in biodiversity. These are called mass extinctions. There are many lesser, yet still dramatic, extinction events, but the five mass extinctions have attracted the most research. An argument can be made that the five mass extinctions are only the five most extreme events in a continuous series of large extinction events throughout the Phanerozoic (since 542 million years ago). In most cases, the hypothesized causes are still controversial; however, the most recent event seems clear.

The Five Mass Extinctions

The fossil record of the mass extinctions was the basis for defining periods of geological history, so they typically occur at the transition point between geological periods. The transition in fossils from one period to another reflects the dramatic loss of species and the gradual origin of new species. These transitions can be seen in the rock strata. [link] provides data on the five mass extinctions.

Mass Extinctions		
Geological Period	**Mass Extinction Name**	**Time (millions of years ago)**
Ordovician–Silurian	end-Ordovician O–S	450–440
Late Devonian	end-Devonian	375–360
Permian–Triassic	end-Permian	251
Triassic–Jurassic	end-Triassic	205
Cretaceous–Paleogene	end-Cretaceous K–Pg (K–T)	65.5

This table shows the names and dates for the five mass extinctions in Earth's history.

The Ordovician-Silurian extinction event is the first recorded mass extinction and the second largest. During this period, about 85 percent of marine species (few species lived outside the oceans) became extinct. The main hypothesis for its cause is a period of glaciation and then warming. The extinction event actually consists of two extinction events separated by about 1 million years. The first event was caused by cooling, and the second event was due to the subsequent warming. The climate changes affected temperatures and sea levels. Some researchers have suggested that a gamma-ray burst, caused by a nearby supernova, is a possible cause of the Ordovician-Silurian extinction. The gamma-ray burst would have stripped away the Earth's ozone layer causing intense ultraviolet radiation from the sun and may account for climate changes observed at the time. The hypothesis is speculative, but extraterrestrial influences on Earth's history are an active line of research. Recovery of biodiversity after the mass extinction took from 5 to 20 million years, depending on the location.

The late Devonian extinction may have occurred over a relatively long period of time. It appears to have affected marine species and not the plants or animals inhabiting terrestrial habitats. The causes of this extinction are poorly understood.

The end-Permian extinction was the largest in the history of life. Indeed, an argument could be made that Earth nearly became devoid of life during this extinction event. The planet looked very different before and after this event. Estimates are that 96 percent of all marine species and 70 percent of all terrestrial species were lost. It was at this time, for example, that the trilobites, a group that survived the Ordovician–Silurian extinction, became extinct. The causes for this mass extinction are not clear, but the leading suspect is extended and widespread

volcanic activity that led to a runaway global-warming event. The oceans became largely anoxic, suffocating marine life. Terrestrial tetrapod diversity took 30 million years to recover after the end-Permian extinction. The Permian extinction dramatically altered Earth's biodiversity makeup and the course of evolution.

The causes of the Triassic–Jurassic extinction event are not clear and hypotheses of climate change, asteroid impact, and volcanic eruptions have been argued. The extinction event occurred just before the breakup of the supercontinent Pangaea, although recent scholarship suggests that the extinctions may have occurred more gradually throughout the Triassic.

The causes of the end-Cretaceous extinction event are the ones that are best understood. It was during this extinction event about 65 million years ago that the dinosaurs, the dominant vertebrate group for millions of years, disappeared from the planet (with the exception of a theropod clade that gave rise to birds). Indeed, every land animal that weighed more then 25 kg became extinct. The cause of this extinction is now understood to be the result of a cataclysmic impact of a large meteorite, or asteroid, off the coast of what is now the Yucatán Peninsula. This hypothesis, proposed first in 1980, was a radical explanation based on a sharp spike in the levels of iridium (which rains down from space in meteors at a fairly constant rate but is otherwise absent on Earth's surface) at the rock stratum that marks the boundary between the Cretaceous and Paleogene periods ([link]). This boundary marked the disappearance of the dinosaurs in fossils as well as many other taxa. The researchers who discovered the iridium spike interpreted it as a rapid influx of iridium from space to the atmosphere (in the form of a large asteroid) rather than a slowing in the deposition of sediments during that period. It was a radical explanation, but the report of an appropriately aged and sized impact crater in 1991 made the hypothesis more believable. Now an abundance of geological evidence supports the theory. Recovery times for biodiversity after the end-Cretaceous extinction are shorter, in geological time, than for the end-Permian extinction, on the order of 10 million years.

Note:
Art Connection

In 1980, Luis and Walter Alvarez, Frank Asaro, and Helen Michels discovered, across the world, a spike in the concentration of iridium within the sedimentary layer at the K–Pg boundary. These researchers hypothesized that this iridium spike was caused by an asteroid impact that resulted in the K–Pg mass extinction. In the photo, the iridium layer is the light band. (credit: USGS)

Scientists measured the relative abundance of fern spores above and below the K–Pg boundary in this rock sample. Which of the following statements most likely represents their findings?

a. An abundance of fern spores from several species was found below the K–Pg boundary, but none was found above.
b. An abundance of fern spores from several species was found above the K–Pg boundary, but none was found below.
c. An abundance of fern spores was found both above and below the K–Pg boundary, but only one species was found below the boundary, and many species were found above the boundary.
d. Many species of fern spores were found both above and below the boundary, but the total number of spores was greater below the boundary.

Note:
Link to Learning

Explore this interactive website about mass extinctions.

The Pleistocene Extinction

The Pleistocene Extinction is one of the lesser extinctions, and a recent one. It is well known that the North American, and to some degree Eurasian, **megafauna**, or large animals, disappeared toward the end of the last glaciation period. The extinction appears to have happened in a relatively restricted time period of 10,000–12,000 years ago. In North America, the losses were quite dramatic and included the woolly mammoths (last dated about 4,000 years ago in an isolated population), mastodon, giant beavers, giant ground sloths, saber-toothed cats, and the North American camel, just to name a few. The possibility that the rapid extinction of these large animals was caused by over-hunting was first suggested in the 1900s. Research into this hypothesis continues today. It seems likely that over-hunting caused many pre-written history extinctions in many regions of the world.

In general, the timing of the Pleistocene extinctions correlated with the arrival of humans and not with climate-change events, which is the main competing hypothesis for these extinctions. The extinctions began in Australia about 40,000 to 50,000 years ago, just after the arrival of humans in the area: a marsupial lion, a giant one-ton wombat, and several giant kangaroo species disappeared. In North America, the extinctions of almost all of the large mammals occurred 10,000–12,000 years ago. All that are left are the smaller mammals such as bears, elk, moose, and cougars. Finally, on many remote oceanic islands, the extinctions of many species occurred coincident with human arrivals. Not all of the islands had large animals, but when there were large animals, they were lost. Madagascar was colonized about 2,000 years ago and the large mammals that lived there became extinct. Eurasia and Africa do not show this pattern, but they also did not experience a recent arrival of humans. Humans arrived in Eurasia hundreds of thousands of years ago after the origin of the species in Africa. This topic remains an area of active research and hypothesizing. It seems clear that even if climate played a role, in most cases human hunting precipitated the extinctions.

Present-Time Extinctions

The sixth, or Holocene, mass extinction appears to have begun earlier than previously believed and has mostly to do with the activities of *Homo sapiens*. Since the beginning of the Holocene period, there are numerous recent extinctions of individual species that are recorded in human writings. Most of these are coincident with the expansion of the European colonies since the 1500s.

One of the earlier and popularly known examples is the dodo bird. The dodo bird lived in the forests of Mauritius, an island in the Indian Ocean. The dodo bird became extinct around 1662. It was hunted for its meat by sailors and was easy prey because the dodo, which did not evolve with humans, would approach people without fear. Introduced pigs, rats, and dogs brought to the island by European ships also killed dodo young and eggs.

Steller's sea cow became extinct in 1768; it was related to the manatee and probably once lived along the northwest coast of North America. Steller's sea cow was first discovered by Europeans in 1741 and was hunted for meat and oil. The last sea cow was killed in 1768. That amounts to 27 years between the sea cow's first contact with Europeans and extinction of the species.

In 1914, the last living passenger pigeon died in a zoo in Cincinnati, Ohio. This species had once darkened the skies of North America during its migrations, but it was hunted and suffered from habitat loss through the clearing of forests for farmland. In 1918, the last living Carolina parakeet died in captivity. This species was once common in the eastern United States, but it suffered from habitat loss. The species was also hunted because it ate orchard fruit when its native foods were destroyed to make way for farmland. The Japanese sea lion, which inhabited a broad area around Japan and the coast of Korea, became extinct in the 1950s due to fishermen. The Caribbean monk seal was distributed throughout the Caribbean Sea but was driven to extinction via hunting by 1952.

These are only a few of the recorded extinctions in the past 500 years. The International Union for Conservation of Nature (IUCN) keeps a list of extinct and endangered species called the Red List. The list is not complete, but it describes 380 extinct species of vertebrates after 1500 AD, 86 of which were driven extinct by overhunting or overfishing.

Estimates of Present-Time Extinction Rates

Estimates of **extinction rates** are hampered by the fact that most extinctions are probably happening without observation. The extinction of a bird or mammal is likely to be noticed by humans, especially if it has been hunted or used in some other way. But there are many organisms that are of less interest to humans (not necessarily of less value) and many that are undescribed.

The background extinction rate is estimated to be about one per million species per year (E/MSY). For example, assuming there are about ten million species in existence, the expectation is that ten species would become extinct each year (each year represents ten million species per year).

One contemporary extinction rate estimate uses the extinctions in the written record since the year 1500. For birds alone this method yields an estimate of 26 E/MSY. However, this value may be underestimated for three reasons. First, many species would not have been described until much later in the time period, so their loss would have gone unnoticed. Second, the number of recently extinct species is increasing because extinct species now are being described from skeletal remains. And third, some species are probably already extinct even though conservationists are reluctant to name them as such. Taking these factors into account raises the estimated extinction rate closer to 100 E/MSY. The predicted rate by the end of the century is 1500 E/MSY.

A second approach to estimating present-time extinction rates is to correlate species loss with habitat loss by measuring forest-area loss and understanding species-area relationships. The **species-area relationship** is the rate at which new species are seen when the area surveyed is increased. Studies have shown that the number of species present increases as the size of the island increases. This phenomenon has also been shown to hold true in other habitats as well. Turning this relationship around, if the habitat area is reduced, the number of species living there will also decline. Estimates of extinction rates based on habitat loss and species-area relationships have suggested that with about 90 percent habitat loss an expected 50 percent of species would become extinct. Species-area estimates have led to species extinction rate calculations of about 1000 E/MSY and higher. In general, actual observations do not show this amount of loss and suggestions have been made that there is a delay in extinction. Recent work has also called into question the applicability of the species-area relationship when estimating the loss of species. This work argues that the species-area relationship leads to an overestimate of extinction rates. A better relationship to use may be the endemics-area relationship. Using this method would bring estimates down to around 500 E/MSY in the coming century. Note that this value is still 500 times the background rate.
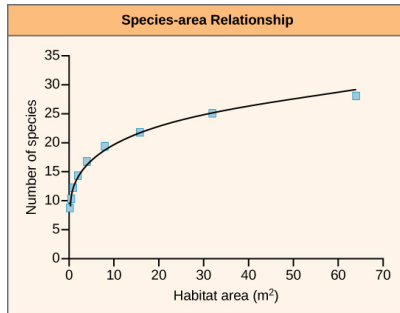
Studies have shown that the number of species present increases with the size of the habitat. (credit: modification of work by Adam B. Smith)

Section Summary

Biodiversity exists at multiple levels of organization and is measured in different ways depending on the goals of those taking the measurements. These measurements include numbers of species, genetic diversity, chemical diversity, and ecosystem diversity. The number of described species is estimated to be 1.5 million with about 17,000 new species being described each year. Estimates for the total number of species on Earth vary but are on the order of 10 million. Biodiversity is negatively correlated with latitude for most taxa, meaning that biodiversity is higher in the tropics. The mechanism for this pattern is not known with certainty, but several plausible hypotheses have been advanced.

Five mass extinctions with losses of more than 50 percent of extant species are observable in the fossil record. Biodiversity recovery times after mass extinctions vary, but have been up to 30 million years. Recent extinctions are recorded in written history and are the basis for one method of estimating contemporary extinction rates. The other method uses measures of habitat loss and species-area relationships. Estimates of contemporary extinction rates vary, but some rates are as high as 500 times the background rate, as determined from the fossil record, and are predicted to rise.

Art Connections

Exercise:

Problem:

[link] Scientists measured the relative abundance of fern spores above and below the K-Pg boundary in this rock sample. Which of the following statements most likely represents their findings?

   a. An abundance of fern spores from several species was found below the K-Pg boundary, but none was found above.
   b. An abundance of fern spores from several species was found above the K-Pg boundary, but none was found below.
   c. An abundance of fern spores was found both above and below the K-Pg boundary, but only one species was found below the boundary , and many species were found above the boundary.
   d. Many species of fern spores were found both above and below the boundary, but the total number of spores was greater below the boundary.

Solution:

[link] A. An abundance of fern spores from several species was found below the K-Pg boundary, but none was found above.

Review Questions

Exercise:

   Problem:

   With an extinction rate of 100 E/MSY and an estimated 10 million species, how many extinctions are expected to occur in a century?

      a. 100
      b. 10, 000
      c. 100, 000
      d. 1, 000, 000

   Solution:

   C

Exercise:

   Problem: An adaptive radiation is_____.

      a. a burst of speciation
      b. a healthy level of UV radiation
      c. a hypothesized cause of a mass extinction
      d. evidence of an asteroid impact

   Solution:

   A

Exercise:

   Problem: The number of currently described species on the planet is about _____.

a. 17,000
   b. 150,000
   c. 1.5 million
   d. 10 million

Solution:

C

Exercise:

Problem:A mass extinction is defined as _____.

   a. a loss of 95 percent of species
   b. an asteroid impact
   c. a boundary between geological periods
   d. a loss of 50 percent of species

Solution:

D

Free Response

Exercise:

Problem: Describe the evidence for the cause of the Cretaceous–Paleogene (K–Pg) mass extinction.

Solution:

The hypothesized cause of the K–Pg extinction event is an asteroid impact. The first piece of evidence of the impact is a spike in iridium (an element that is rare on Earth, but common in meteors) in the geological layers that mark the K–Pg transition. The second piece of evidence is an impact crater off the Yucatán Peninsula that is the right size and age to have caused the extinction event.

Exercise:

Problem: Describe the two methods used to calculate contemporary extinction rates.

Solution:

Extinction rates are calculated based on the recorded extinction of species in the past 500 years. Adjustments are made for unobserved extinctions and undiscovered species. The second method is a calculation based on the amount of habitat destruction and species-area curves.

Glossary

adaptive radiation
    rapid branching through speciation of a phylogenetic tree into many closely related species

biodiversity
    variety of a biological system, typically conceived as the number of species, but also applying to genes, biochemistry, and ecosystems

biodiversity hotspot
    concept originated by Norman Myers to describe a geographical region with a large number of endemic species and a large percentage of degraded habitat

chemical diversity
    variety of metabolic compounds in an ecosystem

ecosystem diversity
    variety of ecosystems

endemic species
    species native to one place

extinction
    disappearance of a species from Earth; local extinction is the disappearance of a species from a region

extinction rate
    number of species becoming extinct over time, sometimes defined as extinctions per million species–years to make numbers manageable (E/MSY)

genetic diversity
    variety of genes in a species or other taxonomic group or ecosystem, the term can refer to allelic diversity or genome-wide diversity

heterogeneity
    number of ecological niches

megafauna
    large animals

species-area relationship
    relationship between area surveyed and number of species encountered; typically measured by incrementally increasing the area of a survey and determining the cumulative numbers of species

The Importance of Biodiversity to Human Life
By the end of this section, you will be able to:

- Identify chemical diversity benefits to humans
- Identify biodiversity components that support human agriculture
- Describe ecosystem services

It may not be clear why biologists are concerned about biodiversity loss. When biodiversity loss is thought of as the extinction of the passenger pigeon, the dodo bird, and even the woolly mammoth, the loss may appear to be an emotional one. But is the loss practically important for the welfare of the human species? From the perspective of evolution and ecology, the loss of a particular individual species is unimportant (however, the loss of a keystone species can lead to ecological disaster). Extinction is a normal part of macroevolution. But the accelerated extinction rate means the loss of tens of thousands of species within our lifetimes, and it is likely to have dramatic effects on human welfare through the collapse of ecosystems and in added costs to maintain food production, clean air and water, and human health.

Agriculture began after early hunter-gatherer societies first settled in one place and heavily modified their immediate environment. This cultural transition has made it difficult for humans to recognize their dependence on undomesticated living things on the planet. Biologists recognize the human species is embedded in ecosystems and is dependent on them, just as every other species on the planet is dependent. Technology smoothes out the extremes of existence, but ultimately the human species cannot exist without its ecosystem.

Human Health

Contemporary societies that live close to the land often have a broad knowledge of the medicinal uses of plants growing in their area. Most plants produce **secondary plant compounds**, which are toxins used to protect the plant from insects and other animals that eat them, but some of which also work as medication. For centuries in Europe, older knowledge about the medical uses of plants was compiled in herbals—books that

identified plants and their uses. Humans are not the only species to use plants for medicinal reasons: the great apes, orangutans, chimpanzees, bonobos, and gorillas have all been observed self-medicating with plants.

Modern pharmaceutical science also recognizes the importance of these plant compounds. Examples of significant medicines derived from plant compounds include aspirin, codeine, digoxin, atropine, and vincristine ([link]). Many medicines were once derived from plant extracts but are now synthesized. It is estimated that, at one time, 25 percent of modern drugs contained at least one plant extract. That number has probably decreased to about 10 percent as natural plant ingredients are replaced by synthetic versions. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.

Catharanthus roseus, the Madagascar periwinkle, has various medicinal properties. Among other uses, it is a source of vincristine, a drug used in the treatment of lymphomas. (credit: Forest and Kim Starr)

In recent years, animal venoms and poisons have excited intense research for their medicinal potential. By 2007, the FDA had approved five drugs based on animal toxins to treat diseases such as hypertension, chronic pain, and diabetes. Another five drugs are undergoing clinical trials, and at least six drugs are being used in other countries. Other toxins under investigation come from mammals, snakes, lizards, various amphibians, fish, snails, octopuses, and scorpions.

Aside from representing billions of dollars in profits, these medicines improve people's lives. Pharmaceutical companies are actively looking for new compounds synthesized by living organisms that can function as medicine. It is estimated that 1/3 of pharmaceutical research and development is spent on natural compounds and that about 35 percent of new drugs brought to market between 1981 and 2002 were from natural compounds. The opportunities for new medications will be reduced in direct proportion to the disappearance of species.

Agricultural Diversity

Since the beginning of human agriculture more than 10,000 years ago, human groups have been breeding and selecting crop varieties. This crop diversity matched the cultural diversity of highly subdivided populations of humans. For example, potatoes were domesticated beginning around 7,000 years ago in the central Andes of Peru and Bolivia. The potatoes grown in that region belong to seven species and the number of varieties likely is in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the diverse demands of the topography, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields.

Potatoes are only one example of human-generated diversity. Every plant, animal, and fungus that has been cultivated by humans has been bred from original wild ancestor species into diverse varieties arising from the demands for food value, adaptation to growing conditions, and resistance to pests. The potato demonstrates a well-known example of the risks of low crop diversity: the tragic Irish potato famine when the single variety grown

in Ireland became susceptible to a potato blight, wiping out the crop. The loss of the crop led to famine, death, and mass emigration. Resistance to disease is a chief benefit to maintaining crop biodiversity, and lack of diversity in contemporary crop species carries similar risks. Seed companies, which are the source of most crop varieties in developed countries, must continually breed new varieties to keep up with evolving pest organisms. These same seed companies, however, have participated in the decline of the number of varieties available as they focus on selling fewer varieties in more areas of the world.

The ability to create new crop varieties relies on the diversity of varieties available and the accessibility of wild forms related to the crop plant. These wild forms are often the source of new gene variants that can be bred with existing varieties to create varieties with new attributes. Loss of wild species related to a crop will mean the loss of potential in crop improvement. Maintaining the genetic diversity of wild species related to domesticated species ensures our continued food supply.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. This system has flaws because, over time, seed banks are lost through accidents, and there is no way to replace them. In 2008, the Svalbard Global Seed Vault ([link]) began storing seeds from around the world as a backup system to the regional seed banks. If a regional seed bank stores varieties in Svalbard, losses can be replaced from Svalbard. The seed vault is located deep into the rock of an arctic island. Conditions within the vault are maintained at ideal temperature and humidity for seed survival, but the deep underground location of the vault in the arctic means that failure of the vault's systems will not compromise the climatic conditions inside the vault.

Note:
Art Connection

The Svalbard Global Seed Vault is a storage facility for seeds of Earth's diverse crops. (credit: Mari Tefre, Svalbard Global Seed Vault)

The Svalbard Global Seed Vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Crop success s is largely dependent on the quality of the soil. Although some agricultural soils are rendered sterile using controversial cultivation and chemical treatments, most contain a huge diversity of organisms that maintain nutrient cycles—breaking down organic matter into nutrient compounds that crops need for growth. These organisms also maintain soil texture that affects water and oxygen dynamics in the soil that are necessary for plant growth. If farmers had to maintain arable soil using alternate means, the cost of food would be much higher than it is now. These kinds of processes are called ecosystem services. They occur within ecosystems, such as soil ecosystems, as a result of the diverse metabolic activities of the organisms living there, but they provide benefits to human food production, drinking water availability, and breathable air.

Other key ecosystem services related to food production are plant pollination and crop pest control. Over 150 crops in the United States require pollination to produce. One estimate of the benefit of honeybee pollination within the United States is $1.6 billion per year; other pollinators contribute up to $6.7 billion more.

Many honeybee populations are managed by apiarists who rent out their hives' services to farmers. Honeybee populations in North America have been suffering large losses caused by a syndrome known as colony collapse disorder, whose cause is unclear. Other pollinators include a diverse array of other bee species and various insects and birds. Loss of these species would make growing crops requiring pollination impossible, increasing dependence on other crops.

Finally, humans compete for their food with crop pests, most of which are insects. Pesticides control these competitors; however, pesticides are costly and lose their effectiveness over time as pest populations adapt. They also lead to collateral damage by killing non-pest species and risking the health of consumers and agricultural workers. Ecologists believe that the bulk of the work in removing pests is actually done by predators and parasites of those pests, but the impact has not been well studied. A review found that in 74 percent of studies that looked for an effect of landscape complexity on natural enemies of pests, the greater the complexity, the greater the effect of pest-suppressing organisms. An experimental study found that introducing multiple enemies of pea aphids (an important alfalfa pest) increased the yield of alfalfa significantly. This study shows the importance of landscape diversity via the question of whether a diversity of pests is more effective at control than one single pest; the results showed this to be the case. Loss of diversity in pest enemies will inevitably make it more difficult and costly to grow food.

Wild Food Sources

In addition to growing crops and raising animals for food, humans obtain food resources from wild populations, primarily fish populations. For approximately 1 billion people, aquatic resources provide the main source of animal protein. But since 1990, global fish production has declined.

Despite considerable effort, few fisheries on the planet are managed for sustainability.

Fishery extinctions rarely lead to complete extinction of the harvested species, but rather to a radical restructuring of the marine ecosystem in which a dominant species is so over-harvested that it becomes a minor player, ecologically. In addition to humans losing the food source, these alterations affect many other species in ways that are difficult or impossible to predict. The collapse of fisheries has dramatic and long-lasting effects on local populations that work in the fishery. In addition, the loss of an inexpensive protein source to populations that cannot afford to replace it will increase the cost of living and limit societies in other ways. In general, the fish taken from fisheries have shifted to smaller species as larger species are fished to extinction. The ultimate outcome could clearly be the loss of aquatic systems as food sources.

Psychological and Moral Value

Finally, it has been argued that humans benefit psychologically from living in a biodiverse world. A chief proponent of this idea is entomologist E. O. Wilson. He argues that human evolutionary history has adapted us to live in a natural environment and that built environments generate stressors that affect human health and well-being. There is considerable research into the

psychological regenerative benefits of natural landscapes that suggests the hypothesis may hold some truth. In addition, there is a moral argument that humans have a responsibility to inflict as little harm as possible on other species.

Section Summary

Humans use many compounds that were first discovered or derived from living organisms as medicines: secondary plant compounds, animal toxins, and antibiotics produced by bacteria and fungi. More medicines are expected to be discovered in nature. Loss of biodiversity will impact the number of pharmaceuticals available to humans.

Crop diversity is a requirement for food security, and it is being lost. The loss of wild relatives to crops also threatens breeders' abilities to create new varieties. Ecosystems provide ecosystem services that support human agriculture: pollination, nutrient cycling, pest control, and soil development and maintenance. Loss of biodiversity threatens these ecosystem services and risks making food production more expensive or impossible. Wild food sources are mainly aquatic, but few are being managed for sustainability. Fisheries' ability to provide protein to human populations is threatened when extinction occurs.

Biodiversity may provide important psychological benefits to humans. Additionally, there are moral arguments for the maintenance of biodiversity.

Art Connections

Exercise:

Problem:

[link] The Svalbard Global Seed Vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Solution:

The ground is permanently frozen so the seeds will keep even if the electricity fails.

Review Questions

Exercise:

Problem:

A secondary plant compound might be used for which of the following?

    a. a new crop variety
    b. a new drug
    c. a soil nutrient
    d. a pest of a crop pest

Solution:

B

Exercise:

Problem: Pollination is an example of _____.

    a. a possible source of new drugs
    b. chemical diversity
    c. an ecosystem service
    d. crop pest control

Solution:

C

Exercise:

Problem:

What is an ecosystem service that performs the same function as a pesticide?

   a. pollination
   b. secondary plant compounds
   c. crop diversity
   d. predators of pests

Solution:

D

Free Response

Exercise:

Problem: Explain how biodiversity loss can impact crop diversity.

Solution:

Crop plants are derived from wild plants, and genes from wild relatives are frequently brought into crop varieties by plant breeders to add valued characteristics to the crops. If the wild species are lost, then this genetic variation would no longer be available.

Exercise:

Problem:

Describe two types of compounds from living things that are used as medications.

Solution:

Secondary plant compounds are toxins produced by plants to kill predators trying to eat them; some of these compounds can be used as drugs. Animal toxins such as snake venom can also be used as drugs. (Alternate answer: antibiotics are compounds produced by bacteria and fungi which can be used to kill bacteria.)

Glossary

secondary plant compound
> compound produced as byproducts of plant metabolic processes that is usually toxic, but is sequestered by the plant to defend against herbivores

Threats to Biodiversity
By the end of this section, you will be able to:

- Identify significant threats to biodiversity
- Explain the effects of habitat loss, exotic species, and hunting on biodiversity
- Identify the early and predicted effects of climate change on biodiversity

The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and resource exploitation. The human population requires resources to survive and grow, and those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are habitat loss, overharvesting, and introduction of exotic species. The first two of these are a direct result of human population growth and resource use. The third results from increased mobility and trade. A fourth major cause of extinction, anthropogenic climate change, has not yet had a large impact, but it is predicted to become significant during this century. Global climate change is also a consequence of human population needs for energy and the use of fossil fuels to meet those needs ([link]). Environmental issues, such as toxic pollution, have specific targeted effects on species, but they are not generally seen as threats at the magnitude of the others.
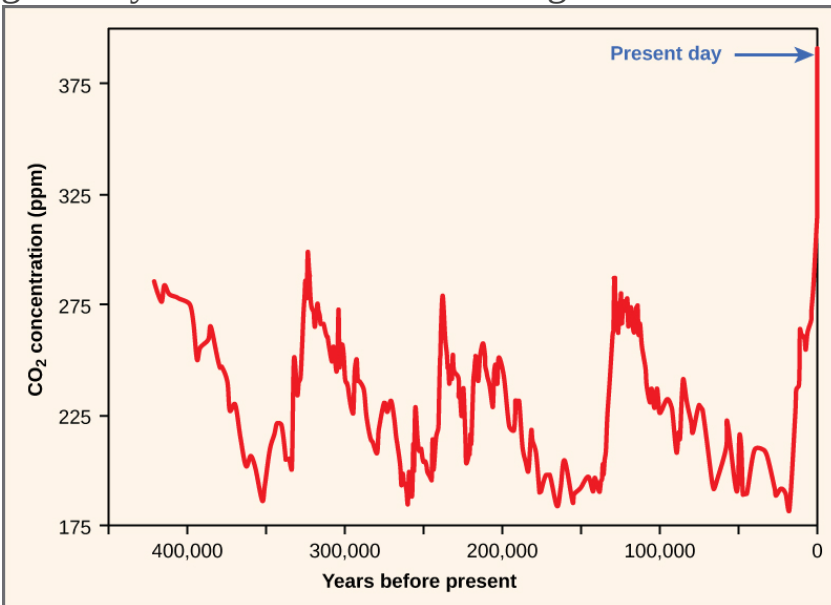
Atmospheric carbon dioxide levels fluctuate in a cyclical manner. However, the burning of fossil fuels in recent history has caused a dramatic increase in the levels of carbon dioxide in the Earth's atmosphere, which have now reached levels never before seen in human history. Scientists predict that the addition of this "greenhouse gas" to the atmosphere is resulting in climate change that will significantly impact biodiversity in the coming century.

Habitat Loss

Humans rely on technology to modify their environment and replace certain functions that were once performed by the natural ecosystem. Other species cannot do this. Elimination of their ecosystem—whether it is a forest, a desert, a grassland, a freshwater estuarine, or a marine environment—will kill the individuals in the species. Remove the entire habitat within the range of a species and, unless they are one of the few species that do well in human-built environments, the species will become extinct. Human destruction of habitats accelerated in the latter half of the twentieth century. Consider the exceptional biodiversity of Sumatra: it is home to one species of orangutan, a species of critically endangered elephant, and the Sumatran tiger, but half of Sumatra's forest is now gone. The neighboring island of Borneo, home to the other species of orangutan, has lost a similar area of forest. Forest loss continues in protected areas of Borneo. The orangutan in Borneo is listed as endangered by the International Union for Conservation of Nature (IUCN), but it is simply the most visible of thousands of species that will not survive the disappearance of the forests of Borneo. The forests are removed for timber and to plant palm oil plantations ([link]). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. A five-year estimate of global forest cover loss for the years 2000–2005 was 3.1 percent. In the humid tropics where forest loss is primarily from timber extraction, 272,000 km^2 was lost out of a global total of

11,564,000 km^2 (or 2.4 percent). In the tropics, these losses certainly also represent the extinction of species because of high levels of endemism.

(a)

(b)

(c)

(d)

(e)

(a) One species of orangutan, *Pongo pygmaeus*, is found only in the rainforests of Borneo, and the other species of orangutan (*Pongo abelii*) is found only in the rainforests of Sumatra. These animals are examples of the exceptional biodiversity of

(c) the islands of Sumatra and Borneo. Other species include the (b) Sumatran tiger (*Panthera tigris sumatrae*) and the (d) Sumatran elephant (*Elephas maximus sumatranus*), both critically endangered species. Rainforest habitat is being removed to make way for (e) oil palm plantations such as this one in Borneo's Sabah Province. (credit a: modification of work by Thorsten Bachner; credit b: modification of work by Dick Mudde; credit c: modification of work by U.S. CIA World Factbook; credit d: modification of work by "Nonprofit Organizations"/Flickr; credit e: modification of work by Dr. Lian Pin Koh)

Note:
Everyday Connection
Preventing Habitat Destruction with Wise Wood Choices
Most consumers do not imagine that the home improvement products they buy might be contributing to habitat loss and species extinctions. Yet the market for illegally harvested tropical timber is huge, and the wood products often find themselves in building supply stores in the United States. One estimate is that 10 percent of the imported timber stream in the United States, which is the world's largest consumer of wood products, is potentially illegally logged. In 2006, this amounted to $3.6 billion in wood products. Most of the illegal products are imported from countries that act as intermediaries and are not the originators of the wood.
How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally? The Forest Stewardship Council (FSC) certifies sustainably harvested forest products, therefore, looking for their certification on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest.

Certification applies to specific products, not to a producer; some producers' products may not have certification while other products are certified. While there are other industry-backed certifications other than the FSC, these are unreliable due to lack of independence from the industry. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal wood products, it is not that simple. Logging and forest management laws vary from country to country; what is illegal in one country may be legal in another. Where and how a product is harvested and whether the forest from which it comes is being maintained sustainably all factor into whether a wood product will be certified by the FSC. It is always a good idea to ask questions about where a wood product came from and how the supplier knows that it was harvested legally.

Habitat destruction can affect ecosystems other than forests. Rivers and streams are important ecosystems and are frequently modified through land development and from damming or water removal. Damming of rivers affects the water flow and access to all parts of a river. Differing flow regimes can reduce or eliminate populations that are adapted to these changes in flow patterns. For example, an estimated 91percent of river lengths in the United States have been developed: they have modifications like dams, to create energy or store water; levees, to prevent flooding; or dredging or rerouting, to create land that is more suitable for human development. Many fish species in the United States, especially rare species or species with restricted distributions, have seen declines caused by river damming and habitat loss. Research has confirmed that species of amphibians that must carry out parts of their life cycles in both aquatic and terrestrial habitats have a greater chance of suffering population declines and extinction because of the increased likelihood that one of their habitats or access between them will be lost.

Overharvesting

Overharvesting is a serious threat to many species, but particularly to aquatic species. There are many examples of regulated commercial fisheries

monitored by fisheries scientists that have nevertheless collapsed. The western Atlantic cod fishery is the most spectacular recent collapse. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s and the pressure on the fishery led to it becoming unsustainable. The causes of fishery collapse are both economic and political in nature. Most fisheries are managed as a common (shared) resource even when the fishing territory lies within a country's territorial waters. Common resources are subject to an economic pressure known as the **tragedy of the commons** in which essentially no fisher has a motivation to exercise restraint in harvesting a fishery when it is not owned by that fisher. The natural outcome of harvests of resources held in common is their overexploitation. While large fisheries are regulated to attempt to avoid this pressure, it still exists in the background. This overexploitation is exacerbated when access to the fishery is open and unregulated and when technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases—whales are an example—economic forces will always drive toward fishing the population to extinction.

Note:
Link to Learning

Explore a U.S. Fish & Wildlife Service [interactive map](#) of critical habitat for endangered and threatened species in the United States. To begin, select "Visit the online mapper."

For the most part, fishery extinction is not equivalent to biological extinction—the last fish of a species is rarely fished out of the ocean. At the same time, fishery extinction is still harmful to fish species and their ecosystems. There are some instances in which true extinction is a possibility. Whales have slow-growing populations and are at risk of complete extinction through hunting. There are some species of sharks with restricted distributions that are at risk of extinction. The groupers are another population of generally slow-growing fishes that, in the Caribbean, includes a number of species that are at risk of extinction from overfishing.

Coral reefs are extremely diverse marine ecosystems that face peril from several processes. Reefs are home to 1/3 of the world's marine fish species —about 4,000 species—despite making up only 1 percent of marine habitat. Most home marine aquaria are stocked with wild-caught organisms, not cultured organisms. Although no species is known to have been driven extinct by the pet trade in marine species, there are studies showing that populations of some species have declined in response to harvesting, indicating that the harvest is not sustainable at those levels. There are concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutan.

Note:
Link to Learning

View a brief video discussing the role of marine ecosystems in supporting human welfare and the decline of ocean ecosystems.

Bush meat is the generic term used for wild animals killed for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten several species with extinction. Traditionally, bush meat in Africa was hunted to feed families directly; however, recent commercialization of the practice now has bush meat available in grocery stores, which has increased harvest rates to the level of unsustainability. Additionally, human population growth has increased the need for protein foods that are not being met from agriculture. Species threatened by the bush meat trade are mostly mammals including many primates living in the Congo basin.

Exotic Species

Exotic species are species that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Such introductions likely occur frequently as natural phenomena. For example, Kudzu (*Pueraria lobata*), which is native to Japan, was introduced in the United States in 1876. It was later planted for soil conservation. Problematically, it grows too well in the southeastern United States—up to a foot a day. It is now a pest species and covers over 7 million acres in the southeastern United States. If an introduced species is able to survive in its new habitat, that introduction is now reflected in the observed range of the species. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems, sometimes at distances that are well beyond the capacity of the species to ever travel itself and outside the range of the species' natural predators.

Most exotic species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, possess preadaptations that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the species that exist there. For this reason, exotic species are also called invasive species. Exotic species can threaten other species through competition for resources, predation, or disease.

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria, as mentioned earlier, the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of cichlids. The accidental introduction of the brown tree snake via aircraft ([link]) from the Solomon Islands to Guam in 1950 has led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are still threatened. The brown tree snake is adept at exploiting human transportation as a means to migrate; one was even found on an aircraft arriving in Corpus Christi, Texas. Constant vigilance on the part of airport, military, and commercial aircraft personnel is required to prevent the snake from moving from Guam to other islands in the Pacific, especially Hawaii. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.

The brown tree snake, *Boiga irregularis,* is an exotic species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950. (credit: NPS)

It now appears that the global decline in amphibian species recognized in the 1990s is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease **chytridiomycosis** ([link]). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed toad (*Xenopus laevis*). It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *Batrachochytrium dendrobatidis* and can act as a reservoir for the disease.

This Limosa Harlequin Frog (*Atelopus limosus*), an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease. (credit: Brian Gratwicke)

Early evidence suggests that another fungal pathogen, *Geomyces destructans*, introduced from Europe is responsible for **white-nose syndrome**, which infects cave-hibernating bats in eastern North America and has spread from a point of origin in western New York State ([link]). The disease has decimated bat populations and threatens extinction of species already listed as endangered: the Indiana bat, *Myotis sodalis*, and potentially the Virginia big-eared bat, *Corynorhinus townsendii virginianus*. How the fungus was introduced is unclear, but one logical presumption would be that recreational cavers unintentionally brought the fungus on clothes or equipment from Europe.

This little brown bat in Greeley Mine, Vermont, March 26, 2009, was found to have white-nose syndrome. (credit: Marvin Moriarty, USFWS)

Climate Change

Climate change, and specifically the anthropogenic (meaning, caused by humans) warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species committed to extinction by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way. The shifting ranges will impose new

competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears. Previously, these two species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring. Changing climates also throw off species' delicate timing adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.

Historic grizzly bear habitat   Extended range of grizzly bear habitat   Polar bear habitat

Since 2008, grizzly bears (*Ursus arctos horribilis*) have been spotted farther north than their historic range, a possible consequence of climate change.

As a result, grizzly bear habitat now overlaps polar bear (*Ursus maritimus*) habitat. The two kinds of bears, which are capable of mating and producing viable offspring, are considered separate species as historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first wild hybrid ever found.

Range shifts are already being observed: for example, some European bird species ranges have moved 91 km northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are not moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The rate of warming appears to be accelerated in the arctic, which is recognized as a serious threat to polar bear populations that require sea ice to hunt seals during the winter months: seals are the only source of protein available to polar bears. A trend to decreasing sea ice coverage has occurred since observations began in the mid-twentieth century. The rate of decline observed in recent years is far greater than previously predicted by climate models.

Finally, global warming will raise ocean levels due to melt water from glaciers and the greater volume of warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species,

and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher elevation mountains—a cycle that has provided freshwater to environments for centuries—will also be jeopardized. This could result in an overabundance of salt water and a shortage of fresh water.

Section Summary

The core threats to biodiversity are human population growth and unsustainable resource use. To date, the most significant causes of extinctions are habitat loss, introduction of exotic species, and overharvesting. Climate change is predicted to be a significant cause of extinctions in the coming century. Habitat loss occurs through deforestation, damming of rivers, and other activities. Overharvesting is a threat particularly to aquatic species, while the taking of bush meat in the humid tropics threatens many species in Asia, Africa, and the Americas. Exotic species have been the cause of a number of extinctions and are especially damaging to islands and lakes. Exotic species' introductions are increasing because of the increased mobility of human populations and growing global trade and transportation. Climate change is forcing range changes that may lead to extinction. It is also affecting adaptations to the timing of resource availability that negatively affects species in seasonal environments. The impacts of climate change are greatest in the arctic. Global warming will also raise sea levels, eliminating some islands and reducing the area of all others.

Art Connections

Exercise:

  Problem:

  Converting a prairie to a farm field is an example of _____.

      a. overharvesting
      b. habitat loss
      c. exotic species

d. climate change

Solution:

B

Review Questions

Exercise:

Problem:

Which two extinction risks may be a direct result of the pet trade?

    a. climate change and exotic species introduction
    b. habitat loss and overharvesting
    c. overharvesting and exotic species introduction
    d. habitat loss and climate change

Solution:

C

Exercise:

Problem:

Exotic species are especially threatening to what kind of ecosystem?

    a. deserts
    b. marine ecosystems
    c. islands
    d. tropical forests

Solution:

C

Free Response

Exercise:

Problem:

Describe the mechanisms by which human population growth and resource use causes increased extinction rates.

Solution:

Human population growth leads to unsustainable resource use, which causes habitat destruction to build new human settlements, create agricultural fields, and so on. Larger human populations have also led to unsustainable fishing and hunting of wild animal populations. Excessive use of fossil fuels also leads to global warming.

Exercise:

Problem:

Explain what extinction threats a frog living on a mountainside in Costa Rica might face.

Solution:

The frog is at risk from global warming shifting its preferred habitat up the mountain. In addition, it will be at risk from exotic species, either as a new predator or through the impact of transmitted diseases such as chytridiomycosis. It is also possible that habitat destruction will threaten the species.

Glossary

bush meat

wild-caught animal used as food (typically mammals, birds, and reptiles); usually referring to hunting in the tropics of sub-Saharan Africa, Asia, and the Americas

chytridiomycosis
disease of amphibians caused by the fungus *Batrachochytrium dendrobatidis;* thought to be a major cause of the global amphibian decline

exotic species
(also, invasive species) species that has been introduced to an ecosystem in which it did not evolve

tragedy of the commons
economic principle that resources held in common will inevitably be overexploited

white-nose syndrome
disease of cave-hibernating bats in the eastern United States and Canada associated with the fungus *Geomyces destructans*

Preserving Biodiversity
By the end of this section, you will be able to:

- Identify new technologies for describing biodiversity
- Explain the legislative framework for conservation
- Describe principles and challenges of conservation preserve design
- Identify examples of the effects of habitat restoration
- Discuss the role of zoos in biodiversity conservation

Preserving biodiversity is an extraordinary challenge that must be met by greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies.
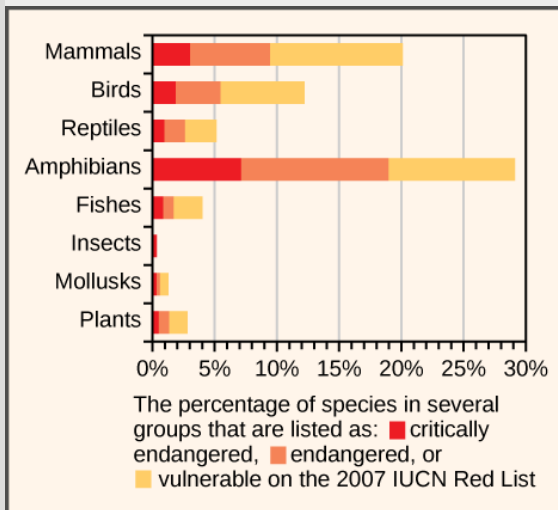
Measuring Biodiversity

The technology of molecular genetics and data processing and storage are maturing to the point where cataloguing the planet's species in an accessible way is close to feasible. **DNA barcoding** is one molecular genetic method, which takes advantage of rapid evolution in a mitochondrial gene present in eukaryotes, excepting the plants, to identify species using the sequence of portions of the gene. Plants may be barcoded using a combination of chloroplast genes. Rapid mass sequencing machines make the molecular genetics portion of the work relatively inexpensive and quick. Computer resources store and make available the large volumes of data. Projects are currently underway to use DNA barcoding to catalog museum specimens, which have already been named and studied, as well as testing the method on less studied groups. As of mid 2012, close to 150,000 named species had been barcoded. Early studies suggest there are significant numbers of undescribed species that looked too much like sibling species to previously be recognized as different. These now can be identified with DNA barcoding.

Numerous computer databases now provide information about named species and a framework for adding new species. However, as already noted, at the present rate of description of new species, it will take close to 500 years before the complete catalog of life is known. Many, perhaps most, species on the planet do not have that much time.

There is also the problem of understanding which species known to science are threatened and to what degree they are threatened. This task is carried out by the non-profit IUCN which, as previously mentioned, maintains the Red List—an online listing of endangered species categorized by taxonomy, type of threat, and other criteria ([link]). The Red List is supported by scientific research. In 2011, the list contained 61,000 species, all with supporting documentation.

Note:
Art Connection

The percentage of species in several groups that are listed as: ■critically endangered, ■endangered, or ■vulnerable on the 2007 IUCN Red List

This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007.

Which of the following statements is not supported by this graph?

a. There are more vulnerable fishes than critically endangered and endangered fishes combined.
b. There are more critically endangered amphibians than vulnerable, endangered and critically endangered reptiles combined.

c. Within each group, there are more critically endangered species than vulnerable species.
d. A greater percentage of bird species are critically endangered than mollusk species.

Changing Human Behavior

Legislation throughout the world has been enacted to protect species. The legislation includes international treaties as well as national and state laws. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) treaty came into force in 1975. The treaty, and the national legislation that supports it, provides a legal framework for preventing approximately 33,000 listed species from being transported across nations' borders, thus protecting them from being caught or killed when international trade is involved. The treaty is limited in its reach because it only deals with international movement of organisms or their parts. It is also limited by various countries' ability or willingness to enforce the treaty and supporting legislation. The illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars. Illegal wildlife trade is monitored by another non-profit: Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC).

Within many countries there are laws that protect endangered species and regulate hunting and fishing. In the United States, the Endangered Species Act (ESA) was enacted in 1973. Species at risk are listed by the Act; the U.S. Fish & Wildlife Service is required by law to develop management plans that protect the listed species and bring them back to sustainable numbers. The Act, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed, or to get an effective management plan in place once it is listed. Additionally, species may be controversially taken off the list without necessarily having had a change in their situation. More fundamentally, the approach to protecting individual species rather than entire ecosystems is both inefficient and focuses efforts on a few highly visible and often charismatic species, perhaps at the expense of other species that go unprotected. At the same

time, the Act has a critical habitat provision outlined in the recovery mechanism that may benefit species other than the one targeted for management.

The Migratory Bird Treaty Act (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers).

The international response to global warming has been mixed. The Kyoto Protocol, an international agreement that came out of the United Nations Framework Convention on Climate Change that committed countries to reducing greenhouse gas emissions by 2012, was ratified by some countries, but spurned by others. Two important countries in terms of their potential impact that did not ratify the Kyoto Protocol were the United States and China. The United States rejected it as a result of a powerful fossil fuel industry and China because of a concern it would stifle the nation's growth. Some goals for reduction in greenhouse gasses were met and exceeded by individual countries, but worldwide, the effort to limit greenhouse gas production is not succeeding. The intended replacement for the Kyoto Protocol has not materialized because governments cannot agree on timelines and benchmarks. Meanwhile, climate scientists predict the resulting costs to human societies and biodiversity will be high.

As already mentioned, the private non-profit sector plays a large role in the conservation effort both in North America and around the world. The approaches range from species-specific organizations to the broadly focused IUCN and TRAFFIC. The Nature Conservancy takes a novel approach. It purchases land and protects it in an attempt to set up preserves for ecosystems. Ultimately, human behavior will change when human values change. At present, the growing urbanization of the human population is a force that poses challenges to the valuing of biodiversity.

Conservation in Preserves

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts. A preserve is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Preserves can be effective in the short term for protecting both species and ecosystems, but they face challenges that scientists are still exploring to strengthen their viability as long-term solutions.

How Much Area to Preserve?

Due to the way protected lands are allocated (they tend to contain less economically valuable resources rather than being set aside specifically for the species or ecosystems at risk) and the way biodiversity is distributed, determining a target percentage of land or marine habitat that should be protected to maintain biodiversity levels is challenging. The IUCN World Parks Congress estimated that 11.5 percent of Earth's land surface was covered by preserves of various kinds in 2003. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes. Research has shown that 12 percent of all species live only outside preserves; these percentages are much higher when only threatened species and high quality preserves are considered. For example, high quality preserves include only about 50 percent of threatened amphibian species. The conclusion must be that either the percentage of area protected must increase, or the percentage of high quality preserves must increase, or preserves must be targeted with greater attention to biodiversity protection. Researchers argue that more attention to the latter solution is required.

Preserve Design

There has been extensive research into optimal preserve designs for maintaining biodiversity. The fundamental principle behind much of the research has been the seminal theoretical work of Robert H. MacArthur and Edward O. Wilson published in 1967 on island biogeography.[footnote] This work sought to understand the factors affecting biodiversity on islands. The fundamental conclusion was that biodiversity on an island was a function of

the origin of species through migration, speciation, and extinction on that island. Islands farther from a mainland are harder to get to, so migration is lower and the equilibrium number of species is lower. Within island populations, evidence suggests that the number of species gradually increases to a level similar to the numbers on the mainland from which the species is suspected to have migrated. In addition, smaller islands are harder to find, so their immigration rates for new species are lower. Smaller islands are also less geographically diverse so there are fewer niches to promote speciation. And finally, smaller islands support smaller populations, so the probability of extinction is higher.

Robert H. MacArthur and Edward O. Wilson, E. O., *The Theory of Island Biogeography* (Princeton, N.J.: Princeton University Press, 1967).

As islands get larger, the number of species accelerates, although the effect of island area on species numbers is not a direct correlation. Conservation preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. For a species to persist in a preserve, the preserve must be large enough. The critical size depends, in part, on the home range that is characteristic of the species. A preserve for wolves, which range hundreds of kilometers, must be much larger than a preserve for butterflies, which might range within ten kilometers during its lifetime. But larger preserves have more core area of optimal habitat for individual species, they have more niches to support more species, and they attract more species because they can be found and reached more easily.

Preserves perform better when there are buffer zones around them of suboptimal habitat. The buffer allows organisms to exit the boundaries of the preserve without immediate negative consequences from predation or lack of resources. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by edges. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing wildlife corridors between them so that individuals and their genes can move between the preserves, for example along rivers and streams, will make the smaller preserves behave more like a large one. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

In addition to the physical, biological, and ecological specifications of a preserve, there are a variety of policy, legislative, and enforcement specifications related to uses of the preserve for functions other than protection of species. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive human recreation. Many of these policy decisions are made based on political pressures rather than conservation considerations. In some cases, wildlife protection policies have been so strict that subsistence-living indigenous populations have been forced from ancestral lands that fell within a preserve. In other cases, even if a preserve is designed to protect wildlife, if the protections are not or cannot be enforced, the preserve status will have little meaning in the face of illegal poaching and timber extraction. This is a widespread problem with preserves in areas of the tropics.

Limitations on Preserves

Some of the limitations on preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, never larger, so setting aside areas that are large enough is difficult. If the area set aside is sufficiently large, there may not be sufficient area to create a buffer around the preserve. In this case, an area on the outer edges of the preserve inevitably becomes a riskier suboptimal habitat for the species in the preserve. Enforcement of protections is also a significant issue in countries without the resources or political will to prevent poaching and illegal resource extraction.

Climate change will create inevitable problems with the location of preserves. The species within them will migrate to higher latitudes as the habitat of the preserve becomes less favorable. Scientists are planning for the effects of global warming on future preserves and striving to predict the need for new preserves to accommodate anticipated changes to habitats; however, the end effectiveness is tenuous since these efforts are prediction based.

Finally, an argument can be made that conservation preserves reinforce the cultural perception that humans are separate from nature, can exist outside of it, and can only operate in ways that do damage to biodiversity. Creating preserves reduces the pressure on human activities outside the preserves to be sustainable and non-damaging to biodiversity. Ultimately, the political, economic, and human demographic pressures will degrade and reduce the size of conservation preserves if the activities outside them are not altered to be less damaging to biodiversity.

Note:
Link to Learning

An interactive global data system of protected areas can be found at website. Review data about individual protected areas by location or study statistics on protected areas by country or region.

Habitat Restoration

Habitat restoration holds considerable promise as a mechanism for restoring and maintaining biodiversity. Of course once a species has become extinct, its restoration is impossible. However, restoration can improve the biodiversity of degraded ecosystems. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity. The wolves ([link]) function to suppress elk and coyote populations and provide more abundant resources to the guild of carrion eaters. Reducing elk populations has allowed revegetation of riparian areas, which has increased the diversity of species in that habitat. Decreasing the coyote population has increased the

populations of species that were previously suppressed by this predator. The number of species of carrion eaters has increased because of the predatory activities of the wolves. In this habitat, the wolf is a keystone species, meaning a species that is instrumental in maintaining diversity in an ecosystem. Removing a keystone species from an ecological community may cause a collapse in diversity. The results from the Yellowstone experiment suggest that restoring a keystone species can have the effect of restoring biodiversity in the community. Ecologists have argued for the identification of keystone species where possible and for focusing protection efforts on those species; likewise, it also makes sense to attempt to return them to their ecosystem if they have been removed.

(a)

(b)

(c)

(d)

(a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The

seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change. (credit a: modification of work by Doug Smith, NPS; credit c: modification of work by Jim Peaco, NPS; credit d: modification of work by "Shiny Things"/Flickr)

Other large-scale restoration experiments underway involve dam removal. In the United States, since the mid-1980s, many aging dams are being considered for removal rather than replacement because of shifting beliefs about the ecological value of free-flowing rivers and because many dams no longer provide the benefit and functions that they did when they were first built. The measured benefits of dam removal include restoration of naturally fluctuating water levels (the purpose of dams is frequently to reduce variation in river flows), which leads to increased fish diversity and improved water quality. In the Pacific Northwest, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports key nutrients to inland ecosystems during its annual spawning migrations. In other regions such as the Atlantic coast, dam removal has allowed the return of spawning anadromous fish species (species that are born in fresh water, live most of their lives in salt water, and return to fresh water to spawn). Some of the largest dam removal projects have yet to occur or have happened too recently for the consequences to be measured. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

The Role of Captive Breeding

Zoos have sought to play a role in conservation efforts both through captive breeding programs and education. The transformation of the missions of zoos from collection and exhibition facilities to organizations that are

dedicated to conservation is ongoing. In general, it has been recognized that, except in some specific targeted cases, captive breeding programs for endangered species are inefficient and often prone to failure when the species are reintroduced to the wild. Zoo facilities are far too limited to contemplate captive breeding programs for the numbers of species that are now at risk. Education is another potential positive impact of zoos on conservation efforts, particularly given the global trend to urbanization and the consequent reduction in contacts between people and wildlife. A number of studies have been performed to look at the effectiveness of zoos on people's attitudes and actions regarding conservation; at present, the results tend to be mixed.

Section Summary

New technological methods such as DNA barcoding and information processing and accessibility are facilitating the cataloging of the planet's biodiversity. There is also a legislative framework for biodiversity protection. International treaties such as CITES regulate the transportation of endangered species across international borders. Legislation within individual countries protecting species and agreements on global warming have had limited success; there is at present no international agreement on targets for greenhouse gas emissions. In the United States, the Endangered Species Act protects listed species but is hampered by procedural difficulties and a focus on individual species. The Migratory Bird Act is an agreement between Canada and the United States to protect migratory birds. The non-profit sector is also very active in conservation efforts in a variety of ways.

Conservation preserves are a major tool in biodiversity protection. Presently, 11percent of Earth's land surface is protected in some way. The science of island biogeography has informed the optimal design of preserves; however, preserves have limitations imposed by political and economic forces. In addition, climate change will limit the effectiveness of preserves in the future. A downside of preserves is that they may lessen the pressure on human societies to function more sustainably outside the preserves.

Habitat restoration has the potential to restore ecosystems to previous biodiversity levels before species become extinct. Examples of restoration include reintroduction of keystone species and removal of dams on rivers. Zoos have attempted to take a more active role in conservation and can have a limited role in captive breeding programs. Zoos also may have a useful role in education.

Art Connections

Exercise:

Problem:

[link] Which of the following statements is not supported by this graph?

- a. There are more vulnerable fishes than critically endangered and endangered fishes combined.
- b. There are more critically endangered amphibians than vulnerable, endangered and critically endangered reptiles combined.
- c. Within each group, there are more critically endangered species than vulnerable species.
- d. A greater percentage of bird species are critically endangered than mollusk species.

Solution:

[link] C

Review Questions

Exercise:

Problem:

Certain parrot species cannot be brought to the United States to be sold as pets. What is the name of the legislation that makes this illegal?

a. Red List
b. Migratory Bird Act
c. CITES
d. Endangered Species Act (ESA)

Solution:

C

Exercise:

Problem:

What was the name of the first international agreement on climate change?

a. Red List
b. Montreal Protocol
c. International Union for the Conservation of Nature (IUCN)
d. Kyoto Protocol

Solution:

D

Exercise:

Problem:

About what percentage of land on the planet is set aside as a preserve of some type?

a. 1 percent

b. 6 percent
c. 11 percent
d. 15 percent

Solution:

C

Free Response

Exercise:

Problem: Describe two considerations in conservation preserve design.

Solution:

Larger preserves will contain more species. Preserves should have a buffer around them to protect species from edge effects. Preserves that are round or square are better than preserves with many thin arms.

Exercise:

Problem:

Describe what happens to an ecosystem when a keystone species is removed.

Solution:

When a keystone species is removed many species will disappear from the ecosystem.

Glossary

DNA barcoding

molecular genetic method for identifying a unique genetic sequence to associate with a species

The Periodic Table of Elements

Periodic Table of the Elements

Group 1	2												13	14	15	16	17	18
1 H 1.01 Hydrogen																		2 He 4.00 Helium
3 Li 6.94 Lithium	4 Be 9.01 Beryllium												5 B 10.81 Boron	6 C 12.11 Carbon	7 N 14.01 Nitrogen	8 O 15.99 Oxygen	9 F 18.99 Fluorine	10 Ne 20.18 Neon
11 Na 22.99 Sodium	12 Mg 24.31 Magnesium	3	4	5	6	7	8	9	10	11	12		13 Al 26.98 Aluminum	14 Si 28.09 Silicon	15 P 30.97 Phosphorus	16 S 32.07 Sulfur	17 Cl 35.45 Chlorine	18 Ar 39.95 Argon
19 K 39.09 Potassium	20 Ca 40.08 Calcium	21 Sc 44.96 Scandium	22 Ti 47.87 Titanium	23 V 50.94 Vanadium	24 Cr 51.99 Chromium	25 Mn 54.94 Manganese	26 Fe 55.85 Iron	27 Co 58.93 Cobalt	28 Ni 58.69 Nickel	29 Cu 63.55 Copper	30 Zn 65.41 Zinc		31 Ga 69.72 Gallium	32 Ge 72.64 Germanium	33 As 74.92 Arsenic	34 Se 78.96 Selenium	35 Br 79.90 Bromine	36 Kr 83.79 Krypton
37 Rb 85.47 Rubidium	38 Sr 87.62 Strontium	39 Y 88.91 Yttrium	40 Zr 91.22 Zirconium	41 Nb 92.91 Niobium	42 Mo 95.94 Molybdenum	43 Tc [98] Technetium	44 Ru 101.1 Ruthenium	45 Rh 102.9 Rhodium	46 Pd 106.4 Palladium	47 Ag 107.9 Silver	48 Cd 112.4 Cadmium		49 In 114.8 Indium	50 Sn 118.7 Tin	51 Sb 121.8 Antimony	52 Te 127.6 Tellurium	53 I 126.9 Iodine	54 Xe 131.3 Xenon
55 Cs 132.9 Cesium	56 Ba 137.3 Barium	57-71 La–Lu *	72 Hf 178.5 Hafnium	73 Ta 180.9 Tantalum	74 W 183.8 Tungsten	75 Re 186.2 Rhenium	76 Os 190.2 Osmium	77 Ir 192.2 Iridium	78 Pt 195.1 Platinum	79 Au 196.9 Gold	80 Hg 200.6 Mercury		81 Tl 204.4 Thallium	82 Pb 207.2 Lead	83 Bi 208.9 Bismuth	84 Po [209] Polonium	85 At [210] Astatine	86 Rn [222] Radon
87 Fr [223] Francium	88 Ra [226] Radium	89-103 Ac–Lr **	104 Rf [261] Rutherfordium	105 Db [262] Dubnium	106 Sg [266] Seaborgium	107 Bh [264] Bohrium	108 Hs [277] Hassium	109 Mt [268] Meitnerium	110 Ds [269] Darmstadtium	111 Rg [272] Roentgenium	112 Cn [285] Copernicium		113 Uut [284] Ununtrium	114 Fl [289] Flerovium	115 Uup [288] Ununpentium	116 Lv [293] Livermorium	117 Uus [294] Ununseptium	118 Uuo [294] Ununoctium

*	57 La 138.9 Lanthanum	58 Ce 140.1 Cerium	59 Pr 140.9 Praseodymium	60 Nd 144.2 Neodymium	61 Pm [145] Promethium	62 Sm 150.4 Samarium	63 Eu 151.9 Europium	64 Gd 157.3 Gadolinium	65 Tb 158.9 Terbium	66 Dy 162.5 Dysprosium	67 Ho 164.9 Holmium	68 Er 167.3 Erbium	69 Tm 168.9 Thulium	70 Yb 173.1 Ytterbium	71 Lu 174.9 Lutetium
**	89 Ac [227] Actinium	90 Th 232.0 Thorium	91 Pa 231.0 Protactinium	92 U 238.0 Uranium	93 Np [237] Neptunium	94 Pu [244] Plutonium	95 Am [243] Americium	96 Cm [247] Curium	97 Bk [247] Berkelium	98 Cf [251] Californium	99 Es [252] Einsteinium	100 Fm [257] Fermium	101 Md [258] Mendelevium	102 No [259] Nobelium	103 Lr [262] Lawrencium

Atomic Number → 1

H ← Symbol

1.01 ← Relative Atomic Mass

Name → Hydrogen

Color Code

- Other non-metals
- Alkali metals
- Transition metals
- Other metals
- Alkaline earth metals
- Halogens
- Noble gases
- Lanthanides
- Actinides
- Unknown chemical properties